

-Rabbits, Hares and Pikas

Status Survey and Conservation Action Plan



Compiled and edited by
Joseph A. Chapman and John E.C. Flux
IUCN/SSC Lagomorph Specialist Group



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Foreword

The IUCN/SSC Lagomorph Specialist Group was constituted in 1978 as part of a determined effort by the Species Survival Commission to broaden the base of its activities by incorporating a large number of new Groups into its membership. By the end of 1979, the Lagomorph Group had attracted from Europe, Asia, Africa, the Americas and the Pacific 19 highly motivated biologists with a concern for problems of conservation of lagomorphs in their respective lands, and a willingness to do something about them.

In August 1979, the young Group held its inaugural meeting at the University of Guelph, Ontario, in conjunction with the first World Lagomorph Conference. The conference emphasized the importance of lagomorphs in world systems and the Proceedings were later published under the auspices of IUCN in a valuable volume distributed by the University.

The Lagomorph Specialist Group reviewed for the first time the status of the world's lagomorphs, critically examined those species which appeared to require attention, and listed important decisions for future conservation action concerning the volcano rabbit *Romerolagus diazi* (Mexico), riverine rabbit *Bunolagus monticularis* (South Africa), hispid hare *Caprolagus hispidus* (India and Nepal), Sumatran rabbit *Nesolagus netscheri* (Indonesia) and Amami rabbit *Pentalagus furnessi* (Japan). Emphasis was placed on the need for a comprehensive taxonomic review of hares and for the development of programs for monitoring lagomorphs and their habitat wherever required. The need to bring these matters to the attention of Governments was given high priority. Project proposals resulting from these deliberations were submitted to the Commission for inclusion in the IUCN Conservation Programme for Sustainable Development.

The Lagomorph Group, building on its good start, soon assumed responsibility for providing the information necessary for preparing and updating lagomorph entries in the Red Data Book and for submissions to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). It holds a strong position against the introduction of the eastern cottontail *Sylvilagus floridanus* to Europe, and has willingly participated in discussions on the subject when requested. The Group also continues to take the lead in keeping lagomorphs on conference agenda at international meetings, and has widened its activities in recent years to look at the status of some of the lesser known races or subspecies of the more common lagomorphs.

Lagomorphs are relatively small mammals and do not excite the curiosity and appeal of some of their larger kind. There has thus never been much financial support for lagomorph conservation. But they are of critical importance in world ecosystems and I applaud the action taken by the Species Survival Commission in setting up this Group when it did. I am particularly pleased that IUCN has agreed to fund this publication of the Lagomorph Specialist Group Action Plan. The achievement of IUCN's main objectives depends to a large extent on the continued activities of small teams of dedicated people like those who constitute this Group; the publication will give them an opportunity to say what they are trying to do.

Ken Myers D.Sc., FIBiol.
Foundation Chairman
IUCN/SSC Lagomorph Specialist Group

Editors' Notes and Acknowledgements

This action plan and review of the status of the world's lagomorphs would not have been possible without the efforts of many people and organisations. This work is truly collaborative in nature and although individuals are listed for each chapter, credit for the entire action plan must be shared. Section Three is the result of the efforts of all of the listed authors, although we make special mention of Andrew Smith whose efforts on the *Ochotona* were immense.

Brad Quayle prepared the maps and figures. Lori Samson and Cindy Howard helped prepare the manuscript. We are grateful to William Oliver for use of his painting of the volcano rabbit as a frontispiece.

Steve Humphrey of the Florida State Museum and Don Wilson of the United States National Museum provided information about some of the little known *Sylvilagus*. Finally, the patience and support of Simon Stuart is gratefully acknowledged, as is the generous support of WWF - The World Wide Fund for Nature - in funding this publication in particular and the SSC Action Planning Programme in general.

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Chapter 1: Introduction and Overview of the Lagomorphs

Joseph A. Chapman and John E.C. Flux

Lagomorphs are found throughout the world either as native or introduced species. They range in size from the small, rodent-like pikas (some less than 100g) to rabbits (one to four kilograms) to the largest hares (in excess of five kilograms).

The harvest of lagomorphs for both sport and commercial use is widespread. Rabbit and hare hunting date back thousands of years in Europe and even today they remain the mainstay of sport hunting in many countries, especially France, Germany and Poland. In North America, the eastern cottontail is the number one game animal, with more cottontails shot and more money and time spent on this species than on any other hunting activity.

Although the number of extant lagomorphs is relatively small in comparison to the rodents, they have been a very successful group. Lagomorphs occur from the equator to 80°N, from sea level to over 5,000m in the mountains and in diverse habitats from desert to tropical forest. There are about 78 living species including 25 pikas, 29 hares and 24 rabbits (Figure 1.1; Table 2.1).

Lagomorphs were originally classified as rodents (*Duplicidentata*) and it was not until 1912 that the order *Lagomorpha* was officially recognized as being distinct from the *Rodentia*. Anatomically, the lagomorphs can be separated

from other rodent-like mammals by the presence of a second set of incisors called “peg” teeth which are located directly behind the upper front incisors. The pikas (ochotonids) have 26 teeth (dental formula i. 2/1, c. O/O, p. 3/2, m. 2/3) and rabbits and hares have 28 teeth (dental formula i. 2/1, c. O/O, p. 3/2, m. 3/3). All lagomorphs possess an elongated rostrum of the skull reinforced by a lattice work of bone (fenestrations), a feature unique to the order (see Figure 1.2).

The pikas are in the monotypic family Ochotonidae, which includes a single genus, *Ochotona*. The jackrabbits and hares are in the family Leporidae and the genus *Lepus*; all are true hares. The rabbits are also in the family Leporidae, but they include the genera *Oryctolagus*, *Sylvilagus*, *Brachylagus*, *Romerolagus*, *Nesolagus*, *Caprolagus*, *Pronolagus*, *Poelagus*, *Bunolagus* and *Pentalagus*. Although many of these genera include species commonly referred to as “hares” (for example the hispid hare) they are all true rabbits.

The pikas are small rodent-like lagomorphs that have a long and distinct ancestry separate from the leporids back to at least the Eocene epoch (50 million years ago). Some early workers suggested that the ochotonids were ancestral to the rabbits and hares, but this does not now appear to be the case. Pikas are highly adapted to their alpine and steppe environ-

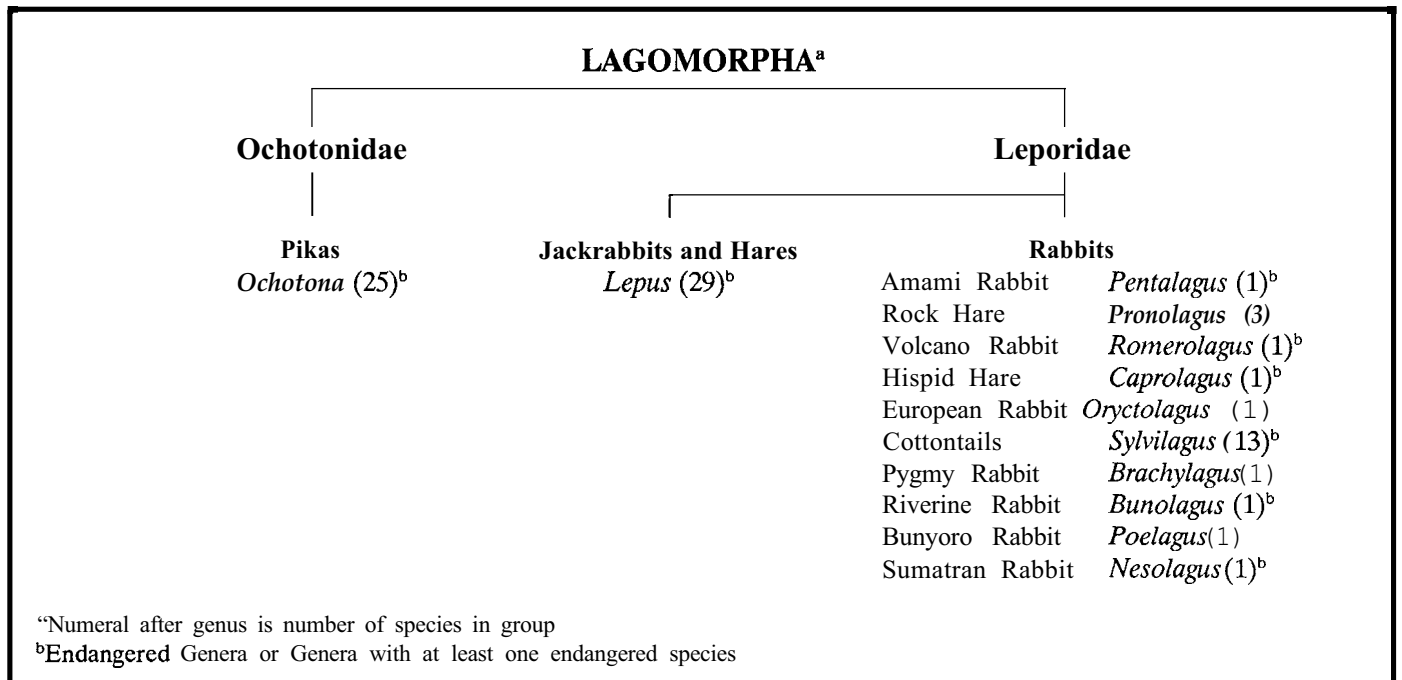


Figure 1.1 Families and genera of the lagomorphs of the world

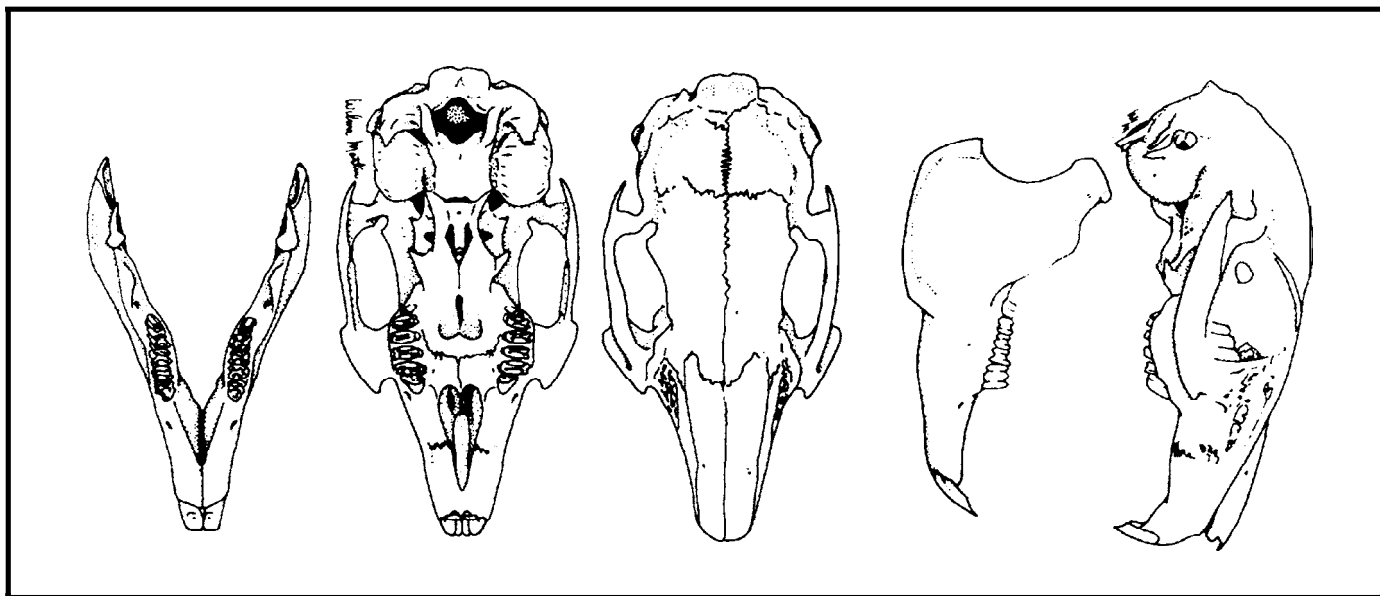


Figure 1.2 Skull of the marsh rabbit *Sylvilagus palustris* from Georgia, United States (NCSM 267). Left: ventral view of cranium and dorsal view of mandible. Centre: dorsal view of cranium. Right: lateral view of cranium and mandible. Drawn by Wilma Martin, and reproduced by permission of the American Society of Mammalogists from *Mammalian Species* no. 153.

ments, both morphologically and behaviorally.

All the Leporidae are adapted for quick movement and flight from danger. Their hind legs are long and adapted to running or bounding (cursorial) locomotion. Their ears are large and moveable to permit detection of approaching danger; in desert forms they are said to function as heat radiators. Some of the larger hares reportedly reach speeds of 80km/h when in full flight and can maintain 50km/h for long periods. Unlike the pikas, their eyes are large and suited to their crepuscular and nocturnal habits. These features are most developed in the hares. Most of the rabbits rely on burrows (warrens) or thick brush cover to avoid predators.

The young of the hares are born fully furred and with their eyes open, in little more than a shallow depression or “form”. On the other hand, rabbits may build nests or elaborate warrens in which to raise their young. These nests are essential because young rabbits are born naked, their eyes tightly closed, and must be cared for by the mother (doe) for up to two to three weeks.

The lagomorphs with the greatest natural distribution (holarctic) are the pikas and hares, although lagomorphs reach their greatest evolutionary diversity in the rabbits. The New World genus *Sylvilagus* (the cottontails), with 13 species, is the most successful group of rabbits from an evolutionary point of view. The European rabbit *Oryctolagus*, although widely introduced and domesticated by man, was historically limited to the Mediterranean region. Other genera such as *Pentalagus* (the Amami rabbit) and *Caprolagus* (the hispid hare) appear to be “primitive” evolutionary branches, now confined to islands or small areas of special habitat. Many of the unusual and little known forms are threatened or endangered.

Objectives

The objectives of this Action Plan are:

1. To provide an overview of the state of knowledge about lagomorphs.
2. To provide a contemporary framework about their importance to man and the world’s ecosystems.
3. To review their status on a worldwide scale.
4. To make recommendations for conservation action to prevent the extinction of any lagomorph species and to allow their populations to recover to safe and productive levels.

Evolution of the Modern Lagomorphs

One question which has interested scientists is, why are there so few lagomorph species (78) relative to rodents (Rodentia 1,685) and even-toed ungulates (Artiodactyla 172)? The best explanation probably has to do with lagomorphs’ slow, conservative diversification in early geological time, leading to bounding locomotion in the rabbits and hares and the small limbs and size of the alpine pikas. Adaptive radiation appears to be occurring in the eastern cottontail *Sylvilagus floridanus* of the neotropics, although this may be because of habitat alterations caused by man.

Only recently have scientists begun to understand and study actively the relationships which exist between the various lagomorph forms. These studies have involved traditional morphological and dental criteria as well as genetic and host-parasite study. Even with this recent work, our best phylogenetic charts are left with major gaps.

For example, the relationship between the cottontails (*Sylvilagus*) and the pygmy rabbit (*Brachylagus*) remains unclear. Some workers consider them to be the most distant of relatives, while others consider them members of the same genus, *Sylvilagus*. Current genetic studies are helping to clarify this question. The dendrogram in Figure 1.3 is based on a composite of the works of many scientists (Dawson 1981, Gureev 1964, among others).

Role in Ecosystems

Lagomorphs make up the base of many predator-prey systems. Their intermediate size and great abundance put them in a position to support a community of small to medium-sized predators. Weasels, foxes, coyotes, cats, civets and many large birds of prey are all sustained by lagomorph populations.

Most lagomorphs are selected for high rates of reproduction ("r"). Their numbers are regulated by extrinsic and intrinsic factors and the dispersal of both young and adults. Lagomorphs have evolved survival mechanisms suited to a

wide variety of environments and situations, but because they are mammalian herbivores low in the food chain, their habitat must provide forage and adequate escape cover. Even so, mortality rates may reach 90% annually in the jackrabbits and hares (*Lepus*), cottontails (*Sylvilagus*), European rabbit (*Oryctolagus*) and steppe-dwelling pikas (*Ochotona*).

In general terms, mortality in lagomorphs can be attributed to predation and disease which result from (1) extreme fluctuations in environmental factors, (2) innate dispersal, (3) density dependent dispersal brought on by limited resources and (4) exhaustion of available plant resources. In temperate and northern latitudes, seasonal climatic variations play an important role as well.

This is exemplified by the modification of reproductive patterns in various latitudes. In New World rabbits (*Sylvilagus* and *Romerolagus*) a direct correlation occurs between latitude and litter-size, with species or subspecies occurring in the north producing the largest litters which are generally correlated with the shortest breeding seasons (Conaway *et al.* 1974). In hares (*Lepus*) the same direct correlation between litter-size and latitude, and inverse correlation between breeding season and latitude, results in an almost constant annual production of young per female for all species (Flux 1981).

Even more interesting is the relationship between latitude and the length of the gestation period. Rabbits occurring in northern latitudes have the shortest gestation periods. The ad-

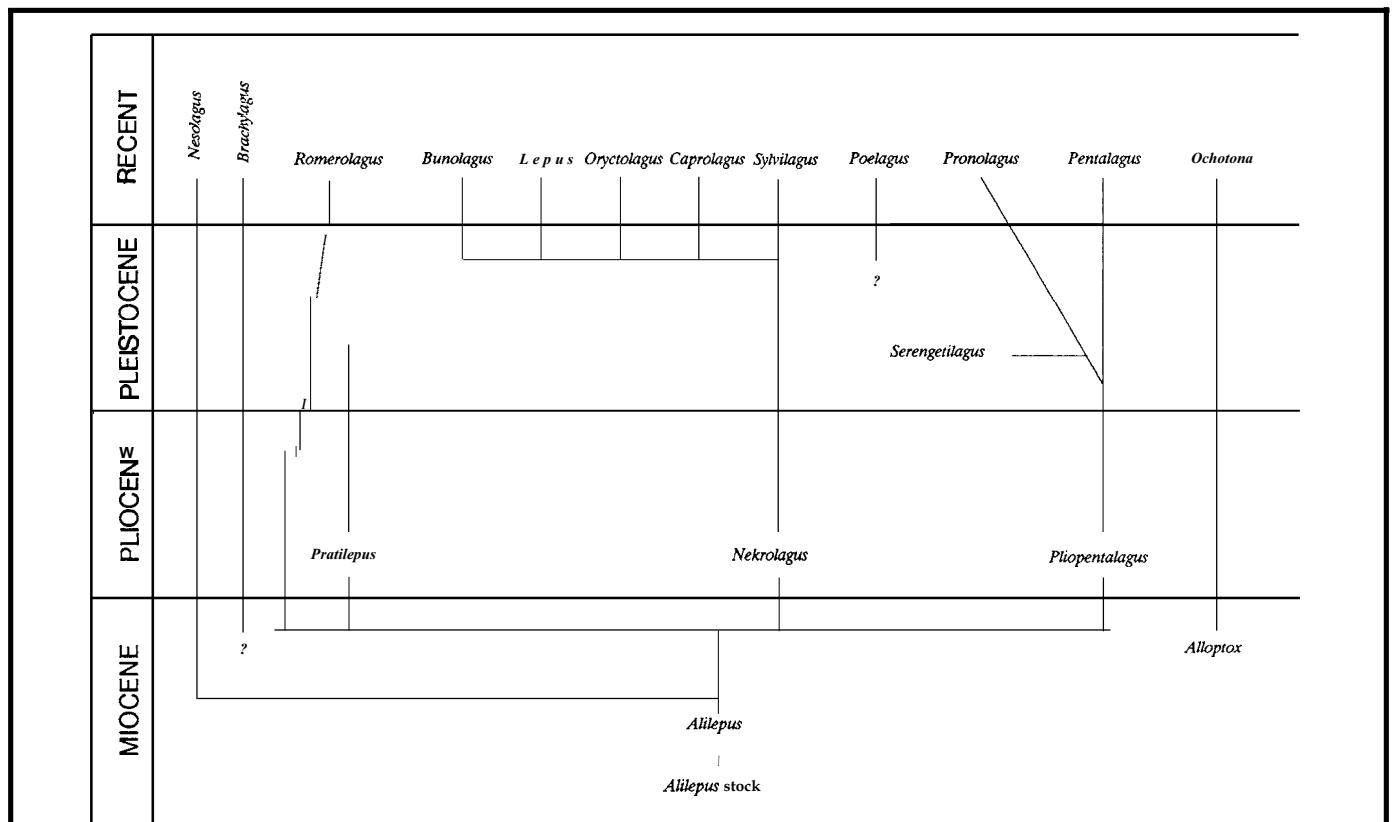


Figure 1.3 Composite phylogeny of the genera of the lagomorpha (based on Dawson 1981, Gureev 1964 and others).

vantage of this arrangement is obvious. At northern locales a shortened gestation period permits the maximum number of young to be produced during the period of most suitable weather. Conversely, it is advantageous for rabbits to have longer gestation periods in subtropical and tropical locales because young rabbits born more fully developed are better able to avoid predators and fend for themselves (Chapman 1984).

Lagomorphs as models for biological and ecological Research

Lagomorphs, especially the rabbits and hares, are ideally suited as models for ecological research. They are the right size and temperament to permit ease of handling, they have high rates of population turnover and they inhabit a broad range of ecologically diverse environments.

For example, Dixon and Chapman (1980) used cottontails to develop new methods of studying home range in vertebrates. The technique, which is called "harmonic mean measure of animal activity," was first used on the brush rabbit *Sylvilagus bachmani* and has already gained wide acceptance for many groups of animals.

The work of Keith (1981) and his colleagues in Wisconsin using snowshoe hare *Lepus americanus*, as models for predator-prey interactions is another example of the use of lagomorphs in ecological research. Fox (1981) and his associates have used the European rabbit *Oryctolagus cuniculus* as a tool in medical research by developing genetically pure races of rabbits for use in studying a variety of inheritable diseases in humans. The vast amount of medical research based on domestic forms of the European rabbit is too well-known to require elaboration.

These are but a few examples of the importance of lagomorphs in research endeavors. Man's interactions with and uses of the lagomorphs can be expected to remain important for very practical reasons.

Lagomorph Behavior

Lagomorph behavioral patterns and displays are as varied as the species themselves.

The behavior of the European rabbit has been studied more than that of any other lagomorph. Much of the work has been done in Australia and the United Kingdom, where rabbit control has been of great importance. There has also been considerable behavioral work on the pikas in Japan, the United States and the Soviet Union. These investigations have been purely scientific in nature, with little emphasis on applied problems. By comparison, there has been relatively little work done on the cottontails and jackrabbits and even less on many of the other genera. For the purpose of this discussion we will consider all three groups of lagomorphs, i.e., pikas, rabbits and hares.

Pikas are highly territorial lagomorphs whose behavioral patterns are remarkably similar throughout their range. Territories are maintained in both sexes by scent marking and vocalizations. They are the only lagomorphs in which vocalizations appear to be highly developed. Perhaps even more interesting is their caching behavior. They store food in "hay piles" which they vigorously defend.

Rabbit behavior varies from the highly territorial, burrowing European rabbit to the non-territorial eastern cottontail *Sylvilagus floridanus*.

The behavior of the cottontails is classified into two main categories: non-social and social behavior. Non-social behavior is commonly observed in lone animals and consists of the following behaviors: exploration, escape, concealment, dusting, loafing, feeding, drinking and grooming. Social behavior is further divided into two categories: the first category is separated into basic male and female postures, vocalizations and movements; and the second category consists of adult social interactions leading to either reproductive or dominant-subordinate interactions (Marsden and Holler 1964).

The social structure of those cottontails studied is based upon a linear dominance hierarchy of the males. The male hierarchy relates to competition between males for estrous females. The intensity of the aggression is proportional to the receptivity of the female and is most intense when the competition is for a female in estrus (Marsden and Holler 1964). Under these conditions, the dominant male is usually able to maintain contact with the female.

Dominant male rabbits enjoy the greatest freedom in the social organization and are involved in the greatest number of male-female interactions. Linear dominance hierarchies for females are not well-defined. However, dominance of unreceptive females over males serves an important reproductive function. This factor is significant during times of nest building, parturition, or nursing, when a male's harassment is detrimental to the female. These hierarchies tend to be quite stable.

Observation of the formation of breeding groups in cottontails suggests that breeding groups form around a nucleus of several females. Female rabbits apparently choose areas within the habitat on the basis of superior food and cover. Sexually active males become associated with these females and form breeding units (Marsden and Holler 1964).

Territoriality occurs in swamp rabbits *Sylvilagus aquaticus* but not in eastern cottontails. Territoriality by dominant males amounts to defense of an area around the females, which follows the localized movements of the breeding group. Synchronized reproduction for the European rabbit and cottontails is well documented.

Female aggression is most likely to occur just prior to the onset of seasonal reproductive behavior and during periods of the seven- or twelve-day sexual cycle. The nearest thing to courtship behavior in cottontails is a dash and jump sequence and related displays (Marsden and Holler 1964, Tefft and Chapman 1987).

The senses are important in the social life of cottontails. Sight is important in its function of recognizing the various

movements and postures of conspecifics. Hearing is suggested as an important sense for swamp rabbits which utilize a series of vocalizations in their behavioral sequences. Vocalizations are also reported for the brush rabbit *Sylvilagus bachmani* and pygmy rabbit *Brachylagus idahoensis*, and are part of the copulatory behavior of the volcano rabbit *Romerolagus diazi* (Tefft and Chapman 1987).

Olfaction is of prime importance in the swamp rabbit and the European rabbit as males sniff spots other rabbits have vacated and, most importantly, follow the trails of females in estrus. Male cottontails nuzzle the anal region of females just prior to parturition and subsequent estrus. This undoubtedly serves as a stimulatory cue to these males of the female's reproductive readiness.

North American jackrabbits and other hares have a complex mating behavior involving fighting between males and between males and females. This "boxing" and rebuff behavior is frequently followed by a sexual chase, during which time the male chases the female in a zigzag manner. Copulation occurs following the chase if the female, which is almost invariably dominant over the male, is receptive (Schneider 1978).

Hares apparently depend more on hearing than sight to avoid danger. Two types of escape response have been noted in jackrabbits: (1) the sneak, in which the hare tries to escape a distant predator by moving into dense vegetation and (2) freezing, in which the hare tries to hide from the predator. When the hare realizes that these responses have failed and it has been seen, it sprints for open country and tries to outrun its pursuer (Dunn et al. 1982).

Vocalizations are also used by hares. Females acting aggressively toward males grunt as they lay their ears back and prepare to strike with the forefeet. Loud high-pitched screams may be given when the animals are handled or caught by predators (Dunn et al. 1982).

All of the lagomorphs groom extensively. Licking the body, cleaning the feet and dusting are all common behaviors. In heavy rain, water is dislodged by vigorous shaking and in wet grass the feet are kicked from time to time to dry them.

Lagomorph Conservation and Management

On a worldwide scale, conservation and management of lagomorphs includes: (1) habitat management, (2) stocking programs, (3) harvest, (4) control and (5) protection.

Habitat management has been most intensive for the North American cottontail. These animals use a wide variety of disturbed, successional and transitional habitats which are readily created by planting, clearing or burning. The essential components of good cottontail habitat are an abundance of well-distributed escape cover interspersed in open grassy areas with abundant forbs. An old pasture is considered among the best habitats for cottontails.

Stocking programs for lagomorphs have occurred virtually

on a worldwide basis, beginning at least 2,000 years ago, and often with less than desirable results. The most notable stocking programs are those which led to the establishment of the European rabbit in Britain, Australia, New Zealand and South America. Others have included the establishment of the European hare in Canada, South America, Australia and New Zealand and cottontails in Europe. The transplanting of lagomorphs from one continent to another can have disastrous consequences, both economic and biological, and should be vigorously opposed.

In North America, stocking programs for the cottontail have been carried out for many years and only recently have sportsmen and others begun to realize the problems associated with the practice. In general, these programs have been carried out with little or no regard for disease transmission, impact on native species, or evaluation of survival of the introduced rabbits. Similarly, in Europe, the translocation of thousands of hares each year continues despite evidence of the futility of this practice.

Chapman and Morgan (1973) have researched and summarized the situation in the mid-Atlantic region of North America. Originally, the southeastern subspecies of the eastern cottontail *S. f. mallurus* was an abundant inhabitant of the glades and river bottoms, while the New England cottontail *S. transitionalis* inhabited woodlands more typical of higher elevations or more northern latitudes. The situation began to change in the 1920's when hunters suspected a decline in cottontail populations. In response wildlife agencies, hunt clubs and private individuals in the region inaugurated a massive program of cottontail importations. Large-scale transplanting began during the 1920's and continued well into the 1950's. Eastern cottontails of several subspecies have been introduced from Kansas, Missouri, Texas and other states into the mid-Atlantic regions. Importations have since diminished, but even today some rabbits are transplanted by private individuals.

In the 1930's Pennsylvania was importing and releasing 50,000 cottontails annually. In the mid-1930's, the folly of such introductions in terms of their failure to support the annual harvest, the general failure of the phenotype released in Pennsylvania and the logistical problems of releasing 50,000 rabbits in an area of 115,000 square kilometers was considered.

During the 1940's, importation programs came under scrutiny from persons concerned about the policy of introducing alien rabbits. They believed that introduced animals could bring new diseases and parasites to the area and that the introduced rabbits might not survive. The importation programs then began to slow. Recent research has shown that introduction programs produced a series of fundamental changes in the populations of the eastern cottontail in the mid-Atlantic region.

Chapman and Fuller (1975) concluded "1. The mid-Atlantic region's native subspecies of eastern cottontail *S. f. mallurus* no longer exists in pure form within the region; interbreeding with introduced rabbits has obliterated the genotype or form, a fact which can be demonstrated genetically and

morphologically. 2. Intergrade eastern cottontails are the inheritors of a genetic vigor which renders them highly efficient colonizers in both stable and changing environments. 3. The native New England cottontail has not interbred freely with the introduced eastern cottontails and has not adapted to changing environmental conditions. 4. Intergrade eastern cottontails are now displacing New England cottontails in the mountainous woodlands of the mid-Atlantic region.”

There have been major and fundamental changes in the rabbit populations of North America. These changes include redistribution of lagomorph species (i.e., transplanting eastern forms to the west coast) and changes in the genetic makeup of resident forms. In Europe and Asia, the long history of translocations of lagomorphs has gone largely unrecorded.

Occasionally lagomorph populations reach densities in which their feeding activities become detrimental to the environment. In North America these problems involve snipping or girdling alpine trees by pikas and snowshoe hares, or damage to agricultural areas by cottontails or more often jackrabbits. In western North America, the jackrabbits occasionally have become rampant pests which required large-scale control.

However, probably the best known control efforts have involved attempts to regulate numbers of the European rabbit in Australia. After years of research a measure of control was obtained by introducing a virus (*Myxoma*) isolated from the forest rabbit *Sylvilagus brasiliensis* of South America. This virus is harmless to the cottontails but is virulent and deadly to the European rabbit.

Following the introduction of myxomatosis into the wild rabbits of Australia, massive die-offs occurred relieving the country of a devastating pest. At present, the rabbits are beginning to develop a level of immunity to the disease and their numbers are starting to increase. At some point the population will reach a balance with the disease. The question is, at what population level? In Britain, 30 years after the introduction of myxomatosis, rabbit numbers are still increasing and now exceed half the pre-myxomatosis levels in many areas.

Five genera of lagomorphs have populations so small or habitats so restricted that complete protection is required. These species include the Amami rabbit *Pentalagus furnessi*, the volcano rabbit *Romerolagus diazi*, the hispid hare *Caprolagus hispidus*, the riverine rabbit *Bunolagus monticularis* and the Sumatran rabbit *Nesolagus netscheri*. The Tehuantepec jackrabbit *Lepus flavigularis*, Tres Marias cottontail *Sylvilagus graysoni*, Omilteme cottontail *S. insonus*, Kozlov's pika *Ochotona koslowi* and the Muli pika *O. muliensis* are also threatened or endangered.

It is apparent that those lagomorphs which are considered rare or endangered are generally monotypic, often relict or isolated species, whose specialized habitat is under threat. Conservation of these forms requires the establishment of natural reserves which will protect these interesting and little known animals.

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Chapter 2: Lagomorph Classification

Renate Angermann, John E.C. Flux, Joseph A. Chapman, Andrew T. Smith

Lagomorphs are a very distinct order of small to medium-sized herbivores. They are now once again considered to be most closely related to rodents (Li *et al* 1987) but there are recognizable fossils of both pikas and rabbits dating back to before the Oligocene.

The order Lagomorpha is characterized by the presence of small peg-like teeth immediately behind the incisors, found in no other mammals. The two families, Ochotonidae and Leporidae, are likewise easily distinguishable. The Ochotonidae (pikas) have hind legs not much longer than the forelegs; are very small; have rounded ears as wide as they are long; and a skull with no supraorbital bones and a relatively short nasal region. The Leporidae, on the other hand, are larger, with hind legs longer than the forelegs; have long ears; and a skull with prominent supraorbital bones and a long nasal region.

Within the Ochotonidae there is only one living genus, *Ochotona* (the pikas), while the Leporidae comprise ten or eleven genera (depending on whether the pygmy rabbit, *Brachylagus*, is recognized as distinct or included within the genus *Sylvilagus*). Most of the genera within the Leporidae are monotypic (that is, they include only a single species) so they pose no taxonomic problem: *Pen talagus* (the Amami rabbit), *Nesolagus* (the Sumatran rabbit), *Romerolagus* (the volcano rabbit), *Oryctolagus* (the European rabbit), *Poelagus* (the Bunyoro rabbit), *Bunolagus* (the riverine rabbit) and *Caprolagus* (the hispid hare). *Pronolagus* includes three species of red rockhares which are restricted to Africa and have so far escaped any taxonomic disputes; but the remaining genus *Lepus* (the jackrabbits and hares) gives rise to many irreconcilable problems.

Standard texts such as Walker's Mammals of the World (4th Edition) and Mammal Species of the World (Honacki, Kinman and Koepl 1982) list 18 to 19 species of *Ochotona* and 19 to 22 species of *Lepus*. The similarity in numbers of species, however, can mask much divergence in the actual names being used. Thus, the four most recent independent lists of *Lepus* names (Angermann 1972, Sokolov 1977, Corbet and Hill 1980 and Honacki *et al.* 1982) "agree" on 19 to 23 species in this genus but use a total of 30 different specific names (see Flux and Angermann 1984, whose suggested revised list of 21 names has also found little general support). A similar problem exists with *Ochotona*, where the close morphological similarities among species have presented major obstacles to taxonomists; one form has been treated as a full species by one author and included in three separate species by others!

The difficulties in taxonomy in *Ochotona* and *Lepus* are only partly attributable to a shortage of material in museums and of taxonomists to collect and study the data; they are also

fundamentally difficult species to deal with. For the *Ochotona* the problem is one of speciation on separate mountain tops or other remote settings where members of a population probably recognize each other by sound rather than sight; hence museum specimens may lack the critical distinguishing feature. The genus is also relatively old, so a profusion of isolated relict species could be expected. In *Lepus*, on the other hand, the difficulty is one of a young, rapidly expanding genus which has found its open grassland habitat becoming widespread through the activity of pastoralists and agriculturalists. Coupled with that is their great mobility; hares can travel 20km in a night and populations may shift hundreds of kilometers if driven by snow or drought. Once again, the critical distinguishing feature is lacking in museum collections: members of a population probably recognize each other primarily by scent.

For the purpose of an action plan it seems necessary to adopt a conservative taxonomy which acknowledges the highest ranking which some recognized specialist has given to that taxa. In effect, we choose to err on the safe side by giving any doubtful species the benefit of the doubt. It is too late, once a population has become extinct, to realize that it was really a unique species and not just a variety of something else. Hence the species checklist which follows includes all those which we, or some lagomorph authority, currently feel are or could be distinct. No list can ever be final and we discuss the conflicting opinions under each species to give the reasons for our selection where possible.

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Table 2.1 Checklist of world lagomorphs

Taxon	Common name	Distribution	Status
ORDER LAGOMORPHA			
Family Ochotonidae (Includes Lagomyidae)			
<i>Ochotona</i> Link, 1795.			
<i>Ochotona alpina</i> (Pallas 1773)	Alpine, or Altai pika	Mountainous areas bordering Gobi Desert on the north (Altai, Sayan, Khangai Mountains, etc.), and south and east of Lake Baikal eastward to the upper Amur River drainage (Kazakh SSR, RSFSR, USSR; MPR; northern Xinjiang, PRC). Isolated population in the Helan Shan, PRC.	Locally common, isolated populations may be threatened.
<i>Ochotona cansus</i> Lyon 1907	Gansu, or Gray pika	Western Shanxi, Southern Shanxi, southwestern Gansu, eastern and southern Qinghai, northwestern Sichuan, PRC.	Locally common, isolated populations may be threatened.
<i>Ochotona collaris</i> (Nelson 1893)	Collared pika	Mountains of central and southern Alaska USA; Northwest Territories and northern British Columbia, Canada.	Locally common.
<i>Ochotona curzoniae</i> (Hodgson 1858)	Black-lipped, or Plateau pika	Southern Xinjiang, Qinghai, Xizang and western Sichuan, PRC; trans-Himalayan Nepal; and Sikkim, India.	Abundant.
<i>Ochotona daurica</i> (Pallas 1776)	Daurian pika	Desert steppes of the Gobi region throughout the MPR and adjacent regions of the USSR and PRC (eastern Qinghai, Gansu, Ningxia, Shanxi, Shaanxi, Nei Mongol, Liaoning, northern Hebei).	Abundant.
<i>Ochotona erythrotis</i> (Bleichner 1890)	Red-eared, or Chinese Red pika	Burchan Budda Mountains of Qinghai to western central Gansu and southern Xinjiang, PRC.	Unknown.
<i>Ochotona forresti</i> Thomas 1923	Forrest's pika	Northwest Yunnan, southeast Xizang, PRC; northern Burma; Assam, Sikkim, India; Bhutan.	Unknown.
<i>Ochotona gaoligongensis</i> Wang, Gong and Duan 1988	Gaoligong pika	Mount Gaoligong, northwest Yunnan Province, PRC.	Unknown.
<i>Ochotona gloveri</i> Thomas 1922	Glover's pika	Southwest Qinghai, northeast Xizang, northwest Yunnan and western Sichuan, PRC.	Unknown.
<i>Ochotona himalayana</i> Feng 1973	Himalayan pika	Mount Jolmolungma (Everest) area, southern Xizang, PRC.	Unknown.
<i>Ochotona hyperborea</i> (Pallas 1811)	Northern, or Siberian pika	Widely distributed in montane taiga of boreal Asia: Ural Mountains, from the east bank of the lower and middle Lena River eastward throughout the Chukotsk and Koryak peninsulas, Kamchatka Peninsula, Sakhalin Island, through the upper Lena River drainage, Transbaikaliya and the Amur region, USSR, the northern mountains of the MPR; the northeastern provinces of the PRC (Nei Mongol, Liaoning, Jilin, Heilongjiang); northern Korea; and northern Japan (Hokkaido).	Abundant.

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Table 2.1 Checklist of world lagomorphs, contd . . .

Taxon	Common name	Distribution	Status
<i>Ochotona iliensis</i> Li and Ma 1986	Ili pika	Borohoro Shan, Xinjiang, PRC.	Unknown.
<i>Ochotona koslowi</i> (Büchner 1894)	Kozlov's pi ka	Arkatag Range, Xinjiang, PRC.	Endangered.
<i>Ochotona Zadacensis</i> (Gunther 1875)	Ladak pika	Mountains of Kashmir, India; Qinghai, Xizang, and Xinjiang, PRC.	Unknown.
<i>Ochotona macrotis</i> (Gunther 1875)	Large-eared pika	Pamir Mountains and western Tien Shan (Tadzhik SSR, Kirgiz SSR, and southeast Kazakh SSR, USSR); Hindu Kush (northeastern Afghanistan); Karakoram Range (Pakistan); Himalayan Mountains (northern India; northern Nepal; Bhutan; adjacent Xizang, PRC); and the Kunlun and associated ranges across central western PRC (Xizang, Xinjiang, Qinghai), and westward into the high mountains of Sichuan and Yunnan, PRC.	Locally common.
<i>Ochotona muliensis</i> Pen and Feng 1962	Muli pika	Western Sichuan, PRC.	Rare and threatened.
<i>Ochotona nubrica</i> Thomas 1922	Nubra pika	Ladak (Pakistan); northern Nepal; Sikkim, India; northern Bhutan; and southern Xizang, PRC.	Unknown.
<i>Ochotona pallasi</i> (Gray 1867)	Pallas's pika	Gobi Desert region from Kazakh SSR, Tuva ASSR, USSR; MPR; western Xinjiang, Nei Mongol, PRC.	Locally abundant, isolated populations may be threatened.
<i>Ochotona princeps</i> (Richardson 1828)	American pika	Mountainous areas throughout western North America (British Columbia, Alberta, Canada; Washington, Oregon, Nevada, California, Idaho, Montana, Wyoming, Utah, Colorado, New Mexico, USA).	Locally common.
<i>Ochotona pusilla</i> (Pallas 1768)	Steppe, or Little pika	Steppe regions from the upper Volga River and southern Ural Mountains south and east to the border of China (RSFSR and Kazakh SSR, USSR).	Locally common, to populations that are rare and declining.
<i>Ochotona roylei</i> (Ogilby 1839)	Royle's pi ka	Along the Himalayan massif from Pakistan; through Kashmir, northwestern India; Nepal; and adjacent Xizang, PRC).	Locally common.
<i>Ochotona rufescens</i> (Gray 1842)	Afghan pika	Patchy distribution in mountains of southern Turkmen SSR, USSR; Iran; Afghanistan; and Baluchistan, Pakistan.	Locally abundant, isolated populations may be threatened.
<i>Ochotona rutila</i> (Severtzov 1873)	Turkestan red pika	Ranges of the Tien Shan, Pamir, Kirgiz (= Alexander the Great), Gissar, and other systems in Uzbek SSR, Kirgiz SSR, Tadzhik SSR and Kazakh SSR, USSR and northern Afghanistan.	Locally common.
<i>Ochotona thibetana</i> (Milne-Edwards 1871)	Moupin pika	Southeastern Qinghai, southern Gansu, southern Shaanxi, western Sichuan, western Hubei, western Yunnan, southern Xizang, PRC; northern Burma; Bhutan; and Sikkim, India.	Locally common, isolated populations may be threatened.
<i>Ochotona thomasi</i> Argyropulo 1948	Thomas's pi ka	Isolated mountain ranges from Gansu, Qinghai, and Sichuan, PRC.	Unknown; likely threatened.

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Table 2.1 Checklist of world lagomorphs, contd . . .

Taxon	Common name	Distribution	Status
Family Leporidae			
<i>Bunolagus</i> Thomas, 1929			
<i>Bunolagus monticularis</i> (Thomas 1903)	Riverine rabbit	Deelfontein and region east of Calvinia (Western and central Karoo), central Cape Province (South Africa).	Rare and endangered.
<i>Caprolagus</i> Blyth, 1845			
<i>Caprolagus hispidus</i> (Pearson 1839)	Hispid hare	Northeast India through southern Himalayas and Nepal, and from Gorkha to Upper Assam (India), Tripura, and Bangladesh.	Rare and endangered.
<i>Lepus</i> Linne, 1758			
<i>Lepus alleni</i> Mearns 1890	Antelope jackrabbit	Southern New Mexico and south central Arizona to northern Nayarit (Mexico); Tiburon Island.	Locally common.
<i>Lepus americanus</i> Erxleben 1777	Snowshoe hare	Southern and central Alaska to southern and central coasts of Hudson Bay to Newfoundland, south to the southern Appalachians, southern Michigan, North Dakota, north central New Mexico, south central Utah, and east central California.	Locally common.
<i>Lepus arcticus</i> Linnaeus 1758	Arctic hare	Arctic North America.	Locally common.
<i>Lepus brachyurus</i> Temminck 1845	Japanese hare	Honshu, Shikoku, Kyushu, Oki Islands and Sado Island (Japan); eastern Siberia (USSR) to Korea.	Locally common.
<i>Lepus californicus</i> Gray 1837	Black-tailed jackrabbit	Hidalgo and southern Queretaro to northern Sonora and Baja California (Mexico), north to southwest Oregon and central Washington, southern Idaho, eastern Colorado, southern South Dakota, Western Missouri, and northwestern Arkansas.	Locally common.
<i>Lepus callotis</i> Wagler 1830 (Includes <i>gaillardii</i> and <i>mexicanus</i>)	White-sided jackrabbit	Central Oaxaca (Mexico) to southeastern Arizona and southwestern New Mexico (USA).	Locally common, declining.
<i>Lepus capensis</i> Linnaeus 1758 (Includes <i>tolai</i> and <i>granatensis</i>)	Cape hare	Africa (in non-forested areas), Spain, from Arabia through central Asia, and the northern half of China to the Pacific coast.	Locally common.
<i>Lepus castroviejo</i> Palacios 1976	Broom hare	Between Sierra de Ancares and de Pena Labra (northern Spain).	Locally common.
<i>Lepus comus</i> Allan 1927	Yunnan hare	Yunnan, southern China	Unknown.
<i>Lepus coreanus</i> Thomas 1892	Korean hare	Korea	Locally common.
<i>Lepus europaeus</i> Pallas 1778	European or brown hare	Open woodland, steppe and subdesert of the Palearctic from southern Sweden and Finland to Britain (introduced to Ireland), through Europe and Asia Minor to the west Siberian lowlands; also introduced into North and South America and Australasia.	Very common.
<i>Lepus fagani</i> Thomas 1902	Ethiopian hare	Ethiopia	Locally common.

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Table 2.1 Checklist of world lagomorphs, contd . . .

Taxon	Common name	Distribution	Status
<i>Lepus flavigularis</i> Wagner 1844	Tehuantepec jackrabbit	Coastal plains and bordering foothills on south end of Isthmus of Tehuantepec (Oaxaca), along Pacific coast to beyond Chiapas (Mexico).	Bare and endangered.
<i>Lepus hubessinicus</i> Hemprich and Ehrenberg 1832	Abyssinian hare	Ethiopia, Somalia.	Locally common.
<i>Lepus hainanus</i> Swinhoe 1870	Hainan hare	Hainan Island only.	Rare.
<i>Lepus insularis</i> Bryant 1891	Black jackrabbit	Espiritu Santo Island (Baja California, Mexico).	No information - restricted.
<i>Lepus mandshuricus</i> Radde 1861	Manchurian hare	Manchuria; North Korea; Amurland (eastern Siberia).	Unknown.
<i>Lepus melainus</i> Li and Luo 1979	Manchurian black hare	Forest of central Manchuria.	Local.
<i>Lepus nigricollis</i> F. Cuvier 1823 (Includes <i>ruficaudatus</i>)	Indian hare	Pakistan; India; Sri Lanka; introduced into Java and Mauritius.	Locally common.
<i>Lepus oiostolus</i> Hodgson 1840	Woolly hare	Northern India to Kansu, Yunnan, and Szechuan (China).	Unknown.
<i>Lepus othus</i> Merriam 1900	Alaskan hare	Coastal lowlands of the Aleutian Island chain and Tundra or alluvial plains of Alaska (USA).	Locally common.
<i>Lepus peguensis</i> Blyth 1855 (Includes <i>siamensis</i>)	Burmese hare	Burma to Indochina.	Unknown.
<i>Lepus saxatilis</i> F Cuvier 1823	Scrub hare	South Africa; Namibia.	Unknown.
<i>Lepus sinensis</i> Gray 1832 (Includes <i>coreanus</i>)	Chinese hare	Southeastern China; Taiwan; South Korea.	Unknown.
<i>Lepus starcki</i> Petter 1963	Ethiopian highland hare	Highlands of central Ethiopia.	Locally common.
<i>Lepus timidus</i> Linnaeus 1758	Mountain, Blue or Snow hare	Paleartic from Scandinavia to Siberia south to Hokkaido, Sikhoto Alin Mountains, Altai, northern Tien Shan, northern Ukraine, and Lithuania; isolated populations in the Alps, Scotland and Ireland.	Locally common.
<i>Lepus townsendii</i> Bachman 1839	White-tailed jackrabbit	Southern Alberta to southwestern Ontario, south to south-western Wisconsin, central Kansas, north central New Mexico, west to central Nevada, east central California, and south central British Columbia.	Locally common.
<i>Lepus victoriae</i> Thomas 1893 (includes <i>crawshayi</i> , <i>whytei</i>)	African savanna hare	Scrub savanna over most of Africa.	Locally common.
<i>Lepus yarkundensis</i> Gunther 1875	Yarkand hare	Steppes of southwestern Sinkiang (Chinese Turkestan).	Rare.

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Table 2.1 Checklist of world lagomorphs, contd . . .

Taxon	Common name	Distribution	Status
<i>Brachylagus</i> Merriam, 1891		Southwest Oregon to east central California, southwestern Utah, north to southeastern Montana; isolated populations in west central Washington; declining .	Locally common.
<i>Brachylagus idahoensis</i> (Merriam 1891)	Pygmy rabbit		
<i>Nesolagus</i> Major, 1899		Sumatra, restricted to montane forest.	Rare and endangered.
<i>Nesolagus netscheri</i> (Schlegel 1880)	Sumatran rabbit		
<i>Oryctolagus</i> Lilljeborg, 1873		Western and southern Europe through the Mediterranean region to Morocco and northern Algeria; present on all continents except Antarctica and many Oceanic islands through introduction.	Very common.
<i>Oryctolagus cuniculus</i> (Linnaeus 1758)	European rabbit		
<i>Pentalagus</i> Lyon, 1904		Amami Island (Japan).	Very rare
<i>Pentalagus furnessi</i> (Stone 1900)	Amami rabbit		
<i>Poelagus</i> St. Leger, 1932		Southern Sudan; northwestern Uganda; northeastern Zaire; Central African Republic; Angola.	Locally common.
<i>Poelagus majorita</i> (St. Leger 1932)	Bunyoro rabbit		
<i>Pronolagus</i> Lyon, 1904		South Africa, in rocky situations.	Locally common.
<i>Pronolagus crassicaudatus</i> (I. Geoffroy 1832)	Greater red rockhare		
<i>Pronolagus randensis</i> Jameson 1907	Jameson's red rockhare	South Africa; eastern Botswana; Zambia; Namibia.	Locally common.
<i>Pronolagus tupestris</i> (A. Smith 1834)	Smith's red rockhare	South Africa to Kenya, in disjunct populations.	Locally common.
<i>Romerolagus</i> Merriam, 1896		Mountain slopes bordering Valley of Mexico near Mexico City.	Rare and endangered.
<i>Romerolagus diazi</i> (Ferrari-Perez 1893)	Teporingo, volcano rabbit		
<i>Sylvilagus</i> Gray, 1867		Eastern Texas and eastern Oklahoma to Alabama and northwestern South Carolina, north to southern Illinois (USA).	Very common.
<i>Sylvilagus aquaticus</i> (Bachman 1837)	Swamp rabbit		
<i>Sylvilagus audubonii</i> (Baird 1858)	Desert or Audubon's cottontail	Northeastern Puebla and western Veracruz to central Montana and southwestern North Dakota, north central Utah, central Nevada, and north central California, south to Baja California and central Sinaloa (Mexico).	Very common.
<i>Sylvilagus bachmani</i> (Waterhouse 1839)	Brush rabbit	Western Oregon (USA) from the Columbia River to Baja California (Mexico), west to Cascade-Sierra Nevada Range.	Very common.
<i>Sylvilagus brasiliensis</i> (Linnaeus 1758)	Forest rabbit, Tapeti	Southern Tamaulipas (Mexico) to Peru, Bolivia, northern Argentina, and southern Brazil.	Locally common.

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Table 2.1 Checklist of world lagomorphs, contd . . .

Taxon	Common name	Distribution	Status
<i>Sylvilagus cunicularius</i> (Waterhouse 1848)	Mexican cottontail	Southern Sinaloa to eastern Oaxaca and Veracruz (Mexico).	Locally common.
<i>Sylvilagus dicei</i> Harris 1932	Dice's cottontail	Mountains of Panama and Costa Rica.	Locally common.
<i>Sylvilagus floridanus</i> (J.A. Allen 1890)	Eastern cottontail	Venezuela to (disjunct in parts of central America) northwestern Arizona, southern Saskatchewan, south central Quebec (Canada), Michigan, Massachusetts and Florida (USA).	Very common.
<i>Sylvilagus graysoni</i> (J.A. Allen 1877)	Tres Marias cottontail	Maria Madre Island, Maria Magdalena Island (Tres Marias Islands, Nayarit, Mexico).	Potentially endangered. Restricted.
<i>Sylvilagus insonus</i> (Nelson 1904)	Omiteme cottontail	Sierra Madre del Sur, central Guerrero (Mexico).	Unknown.
<i>Sylvilagus mansuetus</i> Nelson 1907	San Jose Brush rabbit	Known only from the type locality, San Jose Island, Gulf of California.	Locally common.
<i>Sylvilagus nuttallii</i> (Bachman 1837)	Mountain or Nuttall's cottontail	Intermountain area of North America from southern British Columbia to southern Saskatchewan, south to eastern California, northwestern Nevada, central Arizona, and northwestern New Mexico.	Very common.
<i>Sylvilagus palustris</i> (Bachman 1837)	Marsh rabbit	Florida to southern Virginia (USA) on the coastal plain.	Locally common. <i>S. p. hefneri</i> - endangered
<i>Sylvilagus transitionalis</i> (Bangs 1895)	New England cottontail	Southern Maine to northern Alabama (USA).	Locally common - declining and of special concern in some States

Chapter 3: The Pikas

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Introduction

Pikas (genus *Ochotona*) form a notable and important component of the fauna wherever they now occur in the Northern Hemisphere. Systematically the pikas are a novel group. Living representatives of *Ochotona* form a monotypic genus within the family Ochotonidae, which was clearly differentiated from the other lagomorphs as early as the Oligocene (Wilson 1960, Dawson 1967). Wherever pikas occur they are a phylogenetically independent assay of the forces of natural selection, hence they can provide biologists with an important source of information for comparative analyses. Pikas also represent a robust group for comparisons among taxa (Formozov 1981, Smith 1988). Comparisons among most species of *Ochotona* appear not to be constrained by problems of homology; two separate treatments using different techniques indicate that the major adaptive themes within the genus (species occupying distinctively different habitats) have evolved several times (Vorontsov and Ivanitskaya 1973, Weston 1982). In addition, all species of *Ochotona* are remarkably homogeneous in general morphology and body mass, so that constraints imposed on comparative data by allometric relationships are reduced (Formozov 1981, Smith 1988).

Pikas are also a very poorly known group of mammals. The morphological similarities among species which make them ideal for comparative studies have presented major obstacles to systematists. In addition, most species of pika occur almost exclusively in remote settings, thus biological data needed to support early attempts to classify the genus have generally been lacking. The result has been lack of agreement among all the principal revisers of *Ochotona* (Bonhote 1904, Allen 1938, Ognev 1940, Vinogradov and Argyropulo 1941, Argyropulo 1948, Gureev 1964, Corbet 1978, Honacki, Kinman and Koeppel 1982, Weston 1982, Feng and Zheng 1985, Erbajeva 1988).

This report is the first international attempt to analyze the status of *Ochotona*. The goals are:

- to present a parsimonious systematic treatment of pikas that will prove useful for their conservation and management;
- to summarize the important elements of the biology of each species;

- to define clearly the conservation and management issues concerning pikas.

Pika Systematics

It would be convenient to address the conservation and management issues facing pikas without a detailed consideration of their systematics. However, the confusion which has surrounded most attempts to classify the genus dictates that it is first made clear which forms are included in each species. Comments under the heading "Taxonomy" presented for each species demonstrate that some forms have been commonly included in several species; one form, *forresti*, has been treated as an independent species and placed in three separate species. In addition, the placement of forms (generally subspecies) impinges greatly on the range maps presented for each species.

Some problems in the systematics of pikas are connected with their significant variability in color. Melanistic forms are quite common in talus-dwelling species, especially those that occupy isolated talus patches: alpine pika *O. alpina*, northern pika *O. hyperborea*, large-eared pika *O. macrotis* and American pika *O. princeps*. Probably the insular structure of the rock habitat and the concomitant limited population size of pikas found there yield aberrations in color. In contrast with rock-dwelling species, we know of only a few color aberrations of steppe-dwelling species. There is also partial melanism among pikas, and this condition has also led to systematic confusion among many forms.

The classification of *Ochotona* presented here is unique among published treatments to date, and we are still uncertain of the alignment of many of the species and subspecies. The prevailing philosophy has been to separate forms (split) unless compelling data suggested that they should be synonymised. The rationale for this approach is that for purposes of management it will be easier to combine forms at some later date than to divide them. One of the primary approaches in conservation biology is to define genetically and ecologically distinct units, and this has served as our goal.

Finally, most of the decisions upon which this classification are based hinge on traditional systematic analyses, generally using a restricted number of characters. Only Weston (1982) has used a numerical approach and large numbers of characters in her revision of the genus, but it was a phenetic analysis,

and thus not useful for inferring phylogenetic relationships. The final word on the classification of *Ochotona* should await the use of molecular techniques and cladistic analysis.

Biology and Ecology of Pikas

Several recent reviews have emphasized that most pikas occupy one or another of two discretely different habitat types: 1) non-burrowing talus-dwelling species; and 2) burrowing steppe-, forest- and shrub-dwelling species. A few are intermediate species (those burrowing species which sometimes occupy talus or rock habitat but which also may occur in vegetated habitat devoid of rocks) (Kawamichi 1971a, Formozov 1981, Smith 1981a, 1988). The only distinctive morphological differences between representatives of these two groups appears to be that vibrissae are longer in talus-dwelling pikas, and claws (used for digging) are more powerful and straight in burrowing pikas (Fedosenko 1974, Formozov 1981).

On the other hand, as shown by Smith (1981a, 1988) and in this report, demographic parameters are substantially different between species of talus-dwelling and burrowing *Ochotona*. Litter size and number of litters per year are approximately twice as large in burrowing as in talus-dwelling species of pika. In addition, juvenile pikas in burrowing species may mature and breed in their summer of birth, whereas young first breed as yearlings in talus-dwelling species. Overall, juvenile production by females of burrowing pikas is about one order of magnitude greater than that of talus-dwelling females (Smith 1988).

There are also consistent differences in population density and annual variation in density between talus-dwelling and burrowing species of *Ochotona*. Talus-dwelling pikas live at relatively low densities (generally fewer than ten animals/ha), and their densities do not vary greatly with time. In contrast, population densities of burrowing pikas may be high and fluctuate dramatically (reviewed in Smith 1981a, 1988). In most talus-dwelling species average mortality is low and many individuals live to relatively old ages compared with most small mammals. In burrowing species this trend is reversed: annual mortality is high, few animals live more than two years, and the percentage of yearlings in a population at the beginning of a breeding season is large (Smith 1981a, 1988).

There are also stark contrasts in the degree of social behavior expressed among species of pika inhabiting these two contrasting habitat types. Pikas living in talus tend to be relatively asocial, whereas expression of social behavior is frequent among pikas which inhabit family-controlled burrow systems. There is one further interesting contrast: adult talus-dwelling pikas in North America (American pika *O. princeps* and collared pika *O. collaris*) are individually territorial, whereas Asian talus-dwelling pikas live in pairs on their territories and make communal haypiles (Smith 1981a, 1988).

This brief comparison of species of *Ochotona* indicates that there are two predominant suites of life-history traits.

Talus-dwelling pikas are relatively asocial, comparatively long-lived and have relatively stable low population densities and fecundity rates. In contrast, burrowing pikas normally are highly social, short-lived, may have high but fluctuating population densities, and have high fecundity rates. Preliminary attempts to analyze these dramatic differences among species living in contrasting habitat types have focused on the effects of interspecific competition, habitat productivity, and the degree of protection the habitats may proffer from extreme environmental temperatures (Smith 1981a, 1988).

These comparisons only highlight the effect that habitat may have upon the evolution of pikas. There are many species for which we have few ecological, behavioral or life-history data, and there are some species which do not fit cleanly into the dichotomy presented above. For example, we can learn much from those intermediate species (such as Afghan pika *O. rufescens* and Pallas's pika *O. pallasi*) which can occupy talus or steppe environments. Also, burrowing species living in rhododendron or *Dasiphora* (= *Potentilla*) thickets must have selective pressures which differ significantly from those that burrow in high alpine meadows or desert-like environments. Talus-dwelling pikas can also be subject to different selective pressures, due to contrasting depth of snowpack (Kawamichi 1971a, Millar 1972, Smith 1978, Smith and Ivins 1983a). Perhaps this is why some species are comparatively silent (the large-eared *O. macrotis*, Afghan *O. rufescens* and Turkestan red *O. rutila* pikas) or do not store large amounts of vegetation (large-eared), as do most pikas.

Most of the pikas are restricted to Asia, where there are 23 species. Only two species occur in North America. Among the continents, Asia is unique in having more species of pika than of rabbits and hares. Because of the lack of pika species richness, their role in community dynamics should be evaluated in relation to other taxa (especially rodents and other obligate grazing herbivores). We know of few investigations on this subject. Due to their differences in body mass and corresponding life history traits, it is unlikely that pikas compete directly with sympatric species of rabbits or hares. However, diffuse competition for forage may occur between them because of their reliance on similar vegetation. This subject is unstudied.

Most species within *Ochotona* and *Lepus* do not overlap in range. When two species of *Ochotona* are found in the same area, they normally occupy different habitats (rock, meadow, or shrub), thus reducing opportunity for ecological overlap. Schaller (personal communication) has seen talus-dwelling large-eared *O. macrotis* and steppe-dwelling black-lipped *O. curzoniae* pikas feeding from the same meadow, and in northern Qinghai black-lipped and Gansu *O. cansus* pikas may occur together (Smith and Wang X., unpublished data; Jiang Y. and Wang Z., unpublished data).

The presence of pikas in the ecosystems of Asia is important in terms of generating and maintaining biodiversity due to their role in the food-web. Middle-sized generalist herbivores such as pikas form an important prey base to many carnivorous birds and mammals, either as preferred food or as buffer

species. Most rodents on the Siberian steppe hibernate during winter (Formozov 1966), leaving the non-hibernating lagomorphs as available prey to middle-sized mustelid, felid, or canid carnivores. The steppe-dwelling black-lipped and Daurian *O. daurica* pikas are similar in many respects to the prairie dogs *Cynomys* of North America in biology, and it is possible that the polecat *Mustela eversmanni*, like its counterpart in North America (the black-footed ferret *M. nigripes*), is tied in some way to the dynamics of pika populations (Nekipelov 1954). The populations of all steppe-dwelling pikas may be high in certain years. In those years, pikas are the most important element in the diet of steppe predators. For example, Daurian pikas may comprise the following percentages of the diet of avian predators: steppe eagle *Aquila nipalensis*, 62%; upland buzzard *Buteo hemilasius*, 17%; eagle owl *Bubo bubo*, 73%; and saker falcon *Falco cherrug*, 22% (Peshkov 1957, 1967). Similarly, alpine *O. alpina* and northern *O. hyperborea* pikas are the most important prey for some Mustelidae (weasels *Mustela erminea*, sables *Martes zibellina*, Khlebnikov 1977). In the Altai Mountains, Kazakh SSR, alpine pikas comprise up to 60% of the diet of sables (Sludski *et al.* 1980). In the western Sayan Mountains, Tuva ASSR, 87% of the contents of sable scats are of pikas (Sokolov 1965). Roberts (1977) reported that Afghan pikas were the primary prey of the stone marten *Martes foina* and booted eagle *Hieraaetus pennatus* in Pakistan, whereas in southwestern Turkmenia the levantine viper *Vipera lebitina* appears dependent upon this pika (Danov 1985, Sapargeldyev 1987). Royle's pikas *O. roylei* are a vital food source for stone martens, stoats *Mustela erminea* and Altai weasels *M. altaica* in northern Pakistan (Roberts 1977).

Even larger predators such as wolves *Canis lupus* and brown bears *Ursus arctos* can prey on animals as small as the black-lipped pika (Schaller, personal communication). In fact, pikas form such an important part of the diet of *U. arctos pruinosus* living in Tibet, that when Przewalski (1883) secondarily defined this form, he called it *U. lagomyiarius* or "bear pika-eater." Kozlov (1899) wrote that there were 25 pikas in the stomach of one bear.

The typical caching behavior of pikas also may influence directly the population dynamics of other herbivores that live sympatrically with pikas. Many pika species store large amounts of vegetation in their haypiles (see species accounts later in this chapter). Travina (1984) calculated that even at a modest density of ten to twelve pikas per ha, storage of vegetation by pikas may amount up to 30kg/ha. The stores of Afghan pika may contain up to 58 species of plants and weigh 5kg (Sapargeldyev 1987); near these stores almost all *Artemisia* and *Ephedra* plants appear damaged. Loukashkin (1940) stated that in winter, when snow covered the steppe, Mongolian herdsmen preferentially graze their livestock in areas of high density Daurian pika populations; the tops of the haypiles remain exposed above the surface of the snow and provide food. Melnikov (1974) also noted that domestic cows and horses fed from pika stores in winter. Similarly many native ungulates alter their local distribution in response to pika haypiles. Siberian wapiti *Cervus elaphus sibiricus* and reindeer

Rangifer tarandus tend to accumulate in the habitat of alpine pika in years of heavy snows. Reindeer and snow sheep *Ovis nivicola* feed on the stores of northern pika in winter. Smaller herbivores also focus on pika haypiles: hares *Lepus timidus* and *L. capensis*; marmots *Marmota camtschatica*; and voles *Clethrionomys* spp. Shrews *Sorex* spp. may hunt for invertebrates in haypiles. The density of voles and shrews is four times higher in the vicinity of haypiles of alpine pikas than in the surrounding forest (Naumov 1974).

There may be a competitive relationship between pikas and other grazing herbivores as well. There is an inverse relationship between the density of small rodents and pikas in an area near the middle Lena River where there is a particularly dense population of northern pika. Nevertheless, during winter at this site voles are often caught on the haypiles of pikas (Safronov and Akhremenko 1982).

Pika burrows are often shared with other species of birds and small mammals. The burrows of Afghan pikas are shared with rock-dwelling Persian jird *Meriones persicus*, Libyan jird *M. libycus*, great gerbil *Rhombomys opimus*, mouse-like hamster *Calomyscus mystax*, gray hamster *Cricetulus migratorius* and white-toothed shrews *Crocidura* spp. (Sapargeldyev 1987). In the Mongolian Altai, ground squirrels *Spermophilus undulatus*, gerbils *M. unguiculatus*, and three species of jerboa, as well as hamsters and voles, live in or visit the burrows of Pallas's pika *O. pallasii pricei*. Burrows of the black-lipped pika are the main nesting habitat of several species of birds on the Tibetan plateau: white-rumped snow finch *Montifringilla taczanowskii*, rufous-necked snow finch *M. ruficollis* and Hume's ground jay *Pseudopedocetes humilis* (Smith, unpublished data). Similarly, Pere David's snow finches *Pyrgilauda davidiana* and isabelline wheatears *Oenanthe isabellina* regularly nest in the holes of Daurian pikas (Ivanitski, personal communication).

The burrowing pikas also contribute positively to ecosystem-level dynamics by recycling soil. Fossorial animals in North America increase local primary plant productivity, increase plant species richness, aid in the formation, aeration and mixing of soil, and enhance infiltration of water into the soil (Ellison 1946, Grant, French, and Folse 1980, Grinnell 1923, Tilman 1983). Burrowing mammals do not increase levels of erosion: rather erosion in most cases is caused by overgrazing of vegetation by domestic livestock (Ellison 1946). Few studies have looked at the ecosystem-level effects of pika burrowing in Asia, but some data indicate that the dynamics are similar to the North American studies (investigations on *Microtus brandti*, *Ellobius talpinus*, *Myospalax aspalax* and Daurian pika, Tsendzhav 1980a, b, 1985, Schauer 1987a, b). Jiang and Xia (1985, 1987) determined that the foraging of low and moderate populations of black-lipped pikas on the Qinghai/Xizang steppes is selective and may play an important role in the stabilization of the alpine meadow vegetational community. Local floral diversity is enhanced due to the burrowing of Daurian pikas (Dmitriev 1985, Tsendzhav 1985). Their digging activity loosens and improves the soil, and the accumulation of their excrement and leftover stores in the burrow system yields high levels of organic

materials. Soil temperatures and humidity are higher, and concentrations of nitrogen, calcium and phosphorus are greater near burrow systems than in nearby areas without burrows (Tsendzhav 1985). The result of these interactions is a greater biomass of roots, taller plants, and increased density of plant cover near the burrow system than elsewhere; the overall biomass of plants is almost five times greater when growing over the burrow system than in the surrounding steppe (Tsendzhav 1985). In addition, in spring the phenology of plants growing over burrow systems is ten to fifteen days advanced over plants growing on the nearby steppe. More long-term investigations comparing natural ecosystems with those in which pikas have been controlled (see below) are necessary to evaluate the role of pikas in Asian ecosystems.

The habit of storing food in caches, or haypiles, of rock-dwelling pikas also may influence local vegetative dynamics. The organic remains of pika haypiles stored on talus may facilitate plant colonization on this habitat, and the large accumulation of pika pellets under their shelters gives rise to spots of nitrophylic vegetation (Travina 1984). Certain plants (*Euphorbia altaica*, *Artemesia*, and some crucifers) grow only on the burrows of Pallas's pikas *O. pallasii pricei* (Kholodova 1975, Formozov, unpublished data).

On the other hand, the heavy grazing by pikas in the meadows at the edge of the talus may profoundly alter the composition and diversity of plant communities found there (Khlebnikova 1978, Huntly, Smith and Ivins 1986, Huntly 1987). Foraging by alpine pikas decreases the percentage of flowering plants, decreases the store of seeds in the soil, and slows down succession of the plant community by eating young trees (including *Pinus sibiricus*, the most important element in the Siberian taiga ecosystem) (Khlebnikov and Shtilmark 1965, Loskutov 1966). The American pika, a North American talus-dwelling pika, travels significantly farther into the meadow from the talus border to collect hay than when feeding. Higher proportions of forbs and tall grasses are hayed than eaten directly; the most common plant type eaten is short alpine grasses (Huntly, Smith and Ivins 1986). The result of this selectivity and the differential in distance from talus between haying and feeding is a gradient of plant abundance and species richness that increases with distance from the talus. Unlike most forbs, cushion plants are characteristically maintained close to the talus-meadow interface where it is believed they form an important food for pikas foraging during winter from snow tunnels (Huntly, Smith and Ivins 1986, Huntly 1987).

Economic Importance of Pikas

Pikas have been important, to some extent, for their fur. In the Soviet Union prior to World War II, pika fur was used to produce high quality felt. Now the collection of pika skins for this purpose has ceased because of the nominal return to trappers. In Yakutia, the trapping of northern pika *O. hyperborea* continued until 1953. In some years as many as 14,000 specimens were caught (Tavrovski et al. 1971). In Kazakh

SSR, *Ochotona* was also trapped until the 1950s. All pika species and some gerbils *Rhombomys opimus*, *Meriones tamariscinus* have the same common name in Russian ("pishchukha"). In some years in the Karaganda region (where steppe pika *O. pusilla* and Pallas's pika *O. pallasii* are very common) a few thousand pishchukhas were trapped, but of this total, only 300-350 were really *Ochotona*. These figures indicate that few pikas were trapped throughout Kazakhstan. This hunting has no noticeable influence on the pika populations (Sludski et al. 1980).

Lagomorphs also may compete with man for resources, and in these cases populations may be considered as "pests" and subject to control efforts. Four species of *Ochotona* have been designated as pests, Afghan pika *O. rufescens* for the inclusion in their diet of wheat and other agricultural crops and their tendency to kill or damage apple, walnut and other economically important trees in Baluchistan (Lay 1967, Khokhar and Fulk 1976, Roberts 1977, Khan and Smythe 1980, Khan 1981, Mian 1986, Ahmad, Hussain and Brooks 1987, Mian, Tonsif and Ali 1987, Mian, Ali and Ali 1988, Mian, et al. 1988), and black-lipped, Daurian and Pallas's pikas for their potential competition with domestic livestock on open rangelands (Shi et al. 1984, Schaller 1985, Fan et al. 1986). Control efforts have also been directed at Pallas's pika because it may serve as a vector for plague in select areas of its distributional range in the Soviet Union (Krylova 1976, Shilova et al. 1977). Minor control efforts have been expended on Daurian pika in the southwestern Transbaikalia, USSR. To understand better the role of these pikas in ecosystems dynamics and their conservation biology, each of these control situations is elaborated below.

The Afghan pika is considered a serious pest of apple trees and juniper nurseries in the Ziarat Valley of Baluchistan, Pakistan (Khokhar and Fulk 1976, Khan and Smythe 1980, Khan 1981, Mian 1986, Ahmad, Hussain and Brooks 1987). Normally, in the higher plateau country in central Baluchistan, this species lives in crevices in cliffs and occasionally in burrows under junipers and *Artemesia*. On some of these lands, especially narrow mountain valleys, subsistence crops like barley, wheat, potatoes and animal fodder are now grown. In higher valleys orchards of apples have increased in acreage every year. Pikas are a minor pest of the young green wheat, fodder and vegetable crops grown near their native habitat, and they damage orchard trees seriously (including walnuts and cherries) in winter when green plants are not available. Afghan pikas sometimes completely remove the bark from trees at 25 to 40cm above the ground. The damage varies with the severity of the winter from as little as 0.15% to as much as 5.1% of trees killed and 1.5% to 47.1% damaged per year. Because the losses can amount to hundreds of thousands of dollars (US\$; Ahmad, Hussain and Brooks 1987), the Afghan pika is controlled in these areas.

The subspecies of Pallas's pika *O. pallasii pricei* has been considered a pest in the south of Gorno-Altai Autonomous Oblast and Tuva ASSR, Soviet Union, because it is considered a focus for plague (Krylova 1976, Shilova et al. 1977). Anti-plague stations in Tashanta, Tuva, Kyakhta and Borzya were

established to exterminate both native rodents and lagomorphs. In the Chuiskaya steppe in the southeastern Altai Mountains, several thousand ha were poisoned in the early 1970s (Derevshchikov 1975). Limited experiments with the poison "sevin" in southwestern Tuva showed that this poison sterilized animals and was very harmful to the entire ecosystem, so use of sevin was discontinued. Control of Pallas's pika in this region has now ceased (Erbajeva, personal communication).

The most serious ecosystem-level problem concerning the control of lagomorphs involves black-lipped, Daurian and Pallas's pikas in China. All three species may attain high population densities in meadow-steppe environments (Smith 1988, and this volume). Control began in 1958 with tests on black-lipped pika; large-scale control initiated in 1962 reached a peak between 1963 and 1965 and continues on a reduced scale. No specific data are available on the extent of control of this species, however, it has been estimated that over 13,000,000 ha (200,000,000 mu) were controlled in Qinghai and Gansu Provinces in 1962, prior to the initiation of the largest scale efforts (Fan, personal communication). The heaviest control of Daurian pika occurred later than that of the black-lipped pika. In Qinghai, Gansu and Inner Mongolia about 13,000,000 ha of Daurian pika habitat was controlled in the early years (Fan, personal communication). Most control of Pallas's pika took place in Xinjiang, along the border with Inner Mongolia (330,000 ha; Fan, personal communication). We do not know the total area that has been poisoned for each species or the distribution of effort by year since control was initiated.

The continuous emphasis on control programs from the highest levels of government in China, taken together with the estimates of affected area given above, indicated that extremely large tracts of pastureland in China have been poisoned to kill pikas. Other species, including other non-target pikas (alpine pika *O. alpina argentata*, Gansu pika *O. cansus sorella*, Kozlov's pika *O. koslowi*, Thomas's pika *O. thomasi*), may have been affected by these control efforts.

Chemicals to kill pikas are applied in early spring (before the meadows turn green) or in early winter (after the meadows have dried up). At these times pikas, and other grazing herbivores, are more attracted to poison baits, because food is scarce.

In the early years (when much of the control occurred) the main chemicals used were Compound 1080 and Fussol, applied from hand spreaders, tractors, and often broadcast spreading from airplanes. Application of Fussol was discontinued because of expense and environmental contamination from poisonous secondary derivatives. Use of 1080 continued until 1978 when it was determined that it also killed carnivores that ate pikas (Fan, personal communication).

Because of the importance given to pest control in China, research on poisons has been well-funded, and almost all rodenticides have been tried. In pastureland the primary poisons are now Gophacide and Zinophos. A major emphasis is on the future use of anti-coagulants to avoid secondary

byproducts and damage to the environment. There are, nevertheless, some problems with anti-coagulants: they are expensive and must be distributed in large quantity many times to be effective. Currently the use of anti-coagulants is largely confined to agricultural areas and cities.

Recent research has addressed the ecosystem-level relationships of the three "pest" species of *Ochotona*. Jiang and Xia (1985, 1987) determined that at low and moderate densities, the foraging of black-lipped pikas was selective. Daurian pikas are also selective foragers (Loukashkin 1940, Ognev 1940, Nikolski, Guricheva and Dmitriev 1984). Certain steppe shrubs grow only where Daurian pika burrows are found (Dmitriev 1985). Thus these pika species may play an important role in the stabilization of their respective vegetational communities and contribute to the determination of local floral diversity.

Research has focused on those situations when the black-lipped pika is found at high densities. At these times its diet may overlap extensively with that of domestic animals (Jiang and Xia 1985, 1987). This condition normally occurs at the end of the summer when the pika's reproduction has yielded its highest population density and the meadow vegetation has begun to dry up. There is also an apparent relationship between grazing of domestic animals and pika population density. When the combined grazing of yaks, horses and sheep lower the degree of cover and the height of vegetation, the black-lipped pika may be found at greater densities than on natural meadows (Shi 1983). Similarly, Daurian pikas are more likely to contribute to the deterioration of rangelands that are already overgrazed (Zhong, Zhou and Sun 1985). Apparently under conditions initiated by overgrazing, pikas are in a position to do greater harm to the meadow environment. Shi (1983) concluded that the most effective way to control damage by black-lipped pikas is to improve the condition of the range, which would presumably mean control of the intensity of grazing by domestic animals.

The extensive burrowing by black-lipped and Daurian pikas, particularly when they are at high density, has also been implicated as causing destruction of the grasslands (Jiang and Xia 1985). Apparently no controlled experiments have been conducted to test whether the burrowing activity of pikas may play an important role in soil aeration and nutrient cycling, as has been demonstrated for burrowing mammals in other ecosystems (Ellison 1946, Grant, French and Folse 1980, Grinnell 1923, Tilman 1983, Schauer 1987a, b).

In summary, there has been wide-scale defaunation of vertebrates in Asia as the result of control measures directed at burrowing species of *Ochotona*. This poisoning has drastically altered the natural communities and ecosystems of vast areas of central Asia, and many species of pikas and of other vertebrates have probably been negatively affected. These control measures are continuing. More data are needed on the extent and effect of these control programs. Ultimately it is believed that a goal of restoring natural grazing ecosystems and preserving faunal diversity should be enacted.

Conservation and Management of Pikas

It is unfortunate that the least information is available on the sensitive issue of conservation and management of pikas. Currently no species or forms of *Ochotona* are treated on any national list of endangered or threatened wildlife; however Kozlov's pika is scheduled to be listed as endangered in the forthcoming Red Book for the People's Republic of China. Some European populations of the steppe pika subspecies *O. pusilla pusilla* are listed as rare in the Red Book of the Bashkir Autonomous Republic, Soviet Union (Kuchero 1987). Many species live in such remote and inaccessible areas that their status is unlikely to have been influenced by human activities. In addition to the problems caused by the wide-scale defaunation programs aimed primarily at some pika species (outlined above), this review has uncovered two additional aspects of the conservation and management of pikas which merit detailed consideration: the effects of deforestation; and the results of isolation and small population size found in many forms.

Deforestation

Population pressures throughout Asia have led to the severe alteration of many natural wildlife habitats. Here those instances are summarised where there is a perceived or real threat to populations of lagomorphs in Asia resulting from these changes. There are, in reality, two major classes of habitat alteration affecting lagomorphs. The first is structural changes, such as deforestation or clearing of natural habitats for agriculture. The second, and often related change, is increased insularisation of populations that may lead to their increased vulnerability.

Several species of pika (Gansu, northern *O. hyperborea*, *nubra* *O. nubrica*, steppe, Moupin *O. thibetana*, and Thomas's) occur in forested or shrubby habitat types. Deforestation has been reported widely across Asia, and has been directly implicated in the potential endangerment of Moupin pika subspecies *O. thibetana sikimaria* in its restricted range in the Himalayan massif (R.K. Ghose, personal communication; see that account). At Lachen, Sikkim, India (the type locality), human settlement, terraced cultivation, firewood collection, road construction, etc. have resulted in an almost complete eradication of the thickets of rhododendron that were the preferred habitat of the Moupin pika in this region.

The disappearance of steppe pika subspecies *O. pusilla pusilla* is considered by some scientists to be due to the global change in climate, although others attribute its demise to the destruction of steppe shrubs. It is likely that other populations, as yet uncensused, may be similarly affected (such as *O. cansus sorella*, *O. cansus morosa*, *O. thomasi*).

Isolation and Small Population Sizes

Several species, subspecies and populations of *Ochotona* are isolated and of small population size. In several cases these

isolated forms are poorly known and could be considered endangered if the population history and causes leading to the dangerously small population size were known for certain. Currently Kozlov's pika is scheduled to be listed as endangered in China, but other forms may similarly be affected: alpine pikas *O. alpina argentata*, *O. alpina nitida*, *O. alpina* ssp. nov. (Bajan Ulan Mountains, Mongolia), Gansu pikas *O. cansus sorella*, *O. cansus morosa*, Forrest's pika *O. forresti* (?), Gaoligong pika *O. gaoligongensis*, Himalayan pika *O. himalayana* (?), Ili pika *O. iliensis*, Muli pika *O. muliensis*, Pallas's pikas *O. pallasii hamica*, *O. pallasii pricei* (Choyr Mountains, Mongolia), *O. pallasii sunidica*, American pika *O. princeps goldmani*, *O. princeps nevadensis*, *O. princeps obscura*, *O. princeps tutelata*, Turkestan red pika *O. rutila* (throughout its range), Afghan pika *O. rufescens shukurovi*, Moupin pikas *O. thibetana sikimaria*, *O. thibetana huangensis*, and Thomas' pika *O. thomasi*.

There are several biological reasons for the isolation and small sizes of population found in *Ochotona*. First, most species of pikas are found at high elevations and are adapted to cool alpine/boreal climates. In many places they occur on isolated mountain massifs or individual peaks ("montane islands") surrounded by warmer environments. As climates have become warmer since the Pleistocene the zone which could be occupied on some of these peaks by pikas has become smaller in area, thus leading to smaller population sizes and increased probability of extinction. Detailed analyses of this process in the American pika have shown that pikas currently exist on only five of nineteen montane islands that they once occupied in the Great Basin of the United States (Brown 1971, 1978, Grayson 1977, 1978). The subspecies *O. princeps goldmani*, which lives in ice caves in the lava beds of the Snake River Desert, Idaho, and *O. p. obscura* from mountains in the Big Horn Basin, Wyoming, are similarly isolated. Pikas from the type locality of *O. p. tutelata* in Nevada, have apparently disappeared recently due to a drought in that area (D. J. Hafner and R.M. Sullivan, personal communication). Smith (1974a, 1974b) gives a detailed account on how the interaction of temperature regulation, dispersal, extinction rate of small populations and the availability of suitable habitat may determine the lower limit of the geographical range of the American pika. In the Gobi region of Asia, Kniazev, Savinetski and Sokolovskaya (1986) and Kniazev and Savinetski (1988) have shown that an isolated population of Pallas's pika has gradually decreased in size over time, presumably due to climatic change.

Compounding the effect of temperature on the degree of isolation of pika populations is that many species occupy only talus, a naturally disjunct habitat type. Many of the species accounts given by Ognev (1940) and below document the sporadic distribution of pikas on talus throughout their range. The dynamics of the spatial isolation of pikas on patches of talus has been explored for large-eared, Turkestan red, and American pikas. (Bernstein 1963, 1964, Smith, 1974a, 1980, 1987). Near the lower altitudinal distribution of American pikas, Smith (1974a, 1980, 1987) found that populations on

isolated patches of talus represented dynamic equilibria between extinction (which was inversely related to talus patch size) and recolonization (which was inversely related to inter-patch distance). These isolated populations were often separated by distances of only 50-300m. Regional saturation of habitat decreases when distances between habitat patches increase. Due to this relationship, many pika populations at low elevations may be at risk of local extirpation.

The interplay of the mating system, social structure and dispersal patterns of most species of pikas further ensures that populations remain small and isolated. In general, pikas appear to be monogamous (Smith and Ivins 1984, Formozov 1985, Smith et al. 1986a, 1986b, Smith 1988, and species accounts in this review). In addition, dispersal is restricted in most species which have been investigated (including both talus, American pika, and steppe-dwelling, black-lipped pika forms). Pikas primarily exhibit a philopatric settlement pattern (Smith and Ivins 1983b; A.T. Smith and Wang X.G., unpublished data). Animals which venture away from their natal site encounter frequent hostility, and their likelihood of successful colonization is low unless they can find unoccupied habitat. There are two important consequences of these pat-

terns. First, unoccupied habitats which may even be close to occupied ones may remain vacant for long periods of time because of the low *vagility* of pikas. This behavioral effect compounds the isolation of habitat patches. Second, it may be that most pikas are highly inbred. Electrophoretic data on the American pika demonstrate that within-population genetic variability may be low (Glover et al. 1977, Toliver et al. 1985). Hafner and Sullivan (personal communication) have noted that the isolated population of *O. p. nevadensis* in the Ruby Mountains, Nevada, United States, are monomorphic for a large suite of proteins monitored using electrophoresis.

These aspects of the biology of pikas (elaborated in the species accounts which follow) indicate that populations of talus-dwelling pikas may represent a model system to investigate the effects of 1) genetic population structure, particularly the issue of inbreeding; and 2) small populations and their occupancy of patches of habitat in the testing of extinction theory. Both of these issues are topical in the field of conservation biology, and more empirical data are needed from speciose taxonomic lineages, such as *Ochotona*, to understand fully and predict population-level responses so that correct management decisions on *taxa* of all kinds can be executed.

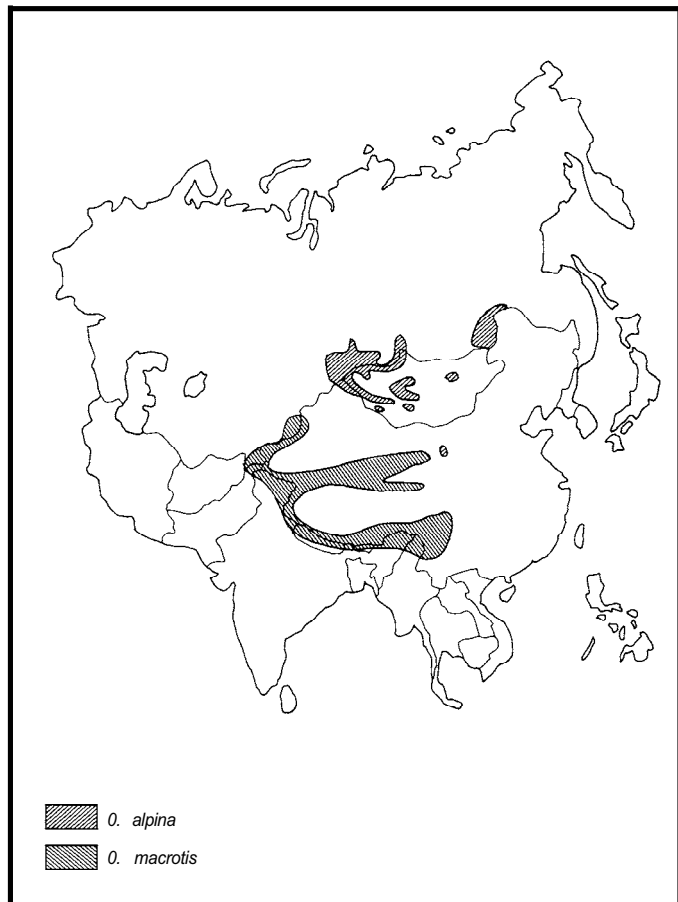


Figure 3.1 Distribution of alpine pika *Ochotona alpina*, and large-eared pika *Ochotona macrotis* in Central Asia

Species Accounts

The following accounts outline the systematic and biological data necessary to understand the conservation and management status of each species. Subspecies names have been listed in alphabetical rather than chronological order. This document highlights the lapses in our knowledge as well as our current understanding of the biology and conservation of pikas. We collectively encourage further research on this fascinating group of mammals.

Alpine or Altai Pika *Ochotona alpina* (Pallas 1773)

Subspecies: *Ochotona alpina alpina* (Pallas 1773) (includes *Lagomys ater*); *Ochotona alpina argentata* Howell 1928; *Ochotona alpina changaica* Ognev 1940; *Ochotona alpina cinereofusca* (Schrenck 1858); *Ochotona alpina nitida* Hollister 1912a; *Ochotona alpina scorodumovi* Skalon 1935; *Ochotona alpina sushkini* Thomas 1924

Taxonomy

The alpine pika has been considered to include northern pika *O. hyperborea* (Vinogradov and Argyropulo 1941, Argyropulo 1948, Gureev 1964, Corbet 1978, Honacki, Kinman and Koepl 1982, Weston 1982, Feng and Zheng 1985) and the North American forms, American *O. princeps* and collared *O. collaris* pikas (Argyropulo 1948, Gureev 1964, Corbet 1978). Here these four forms are treated as separate species (see Corbet and Hill 1986). Weston (1981) determined that the North American forms are significantly different morphologi-

cally from the Asian forms. Authorities who have had the opportunity to investigate alpine and northern pikas closely comment on their noticeable differences throughout their zone of sympatry (Ognev 1940, Sokolov and Orlov 1980). In addition, diploid chromosome number differs between the two species (2N = 42 in the alpine and 40 in the northern pika) (Vorontsov and Ivanitskaya 1973).

The assignment of subspecies to the alpine pika followed here was based on the form having been included in *O. alpina* by one or more of those authorities who distinguished between *O. alpina* and *O. hyperborea*: Ognev (1940), Bobrinski, Kuznetsov and Kuzyakin (1944), Ellerman and Morrison-Scott (1951). In addition, one of us (RSH) has examined specimens representing all named subspecies (and most holotypes) in order to confirm published accounts.

Formozov and Nikolski (1979) argued that the form *svatoshi*, often placed in *alpina*, should be transferred to the northern pika *O. hyperborea*. Not only *svatoshi*, but also *cinereofusca* and *scorodumovi* are problematical. These pikas live between the Shilka and Argun rivers. They are close to the alpine pika in their morphology and short call characteristics, but other features of their vocal repertoire differ from typical *alpina* (Formozov and Yakhontov 1988). It is likely that individual specimens from the zone of sympatry have been misidentified in museum collections and caution should be used. At present, we accept the assignment of *svatoshi* to *O. hyperborea*, but provisionally retain *cinereofusca* and *scorodumovi* in *O. alpina*.

Another form, *O. sushkini*, was originally described by Thomas (1924) as being most nearly allied to *O. pricei* [= *O. pallasi*]. Subsequently authors have considered *sushkini* a subspecies of Pallas's pika *O. pallasi*. However, our comparison of the type series of *sushkini* in the British Museum (Natural History) (BMNH) with a series of typical *alpina* and *pallasi* yields the following distinctions. While the skulls are difficult to distinguish (as pointed out by Ellerman and Morrison-Scott 1951), the interorbital width of *pallasi* is less than in *alpina*, and the pelage and soles of the feet are pale in *pallasi* but dark gray to brownish (varying seasonally) in *alpina*. Additionally, the type locality of *sushkini* lies outside of the range of *O. pallasi* in the Altai Mountains (Yudin, Galkina and Potapkina 1979). The holotype of *sushkini* is assignable to *alpina*; *sushkini* was also placed in *O. alpina* by Pavlinov and Rossolimo (1987) and Erbajeva (1988).

Status and Summary

The subspecies *Ochotona alpina argentata* (known only from the type locality in the Helan Shan near the border of Ningxia, Hexizoulang and Gansu provinces, China) is known from only a few specimens and has not been collected for over half a century, it has, however, recently been seen (Wulsin, unpubl. field notes, NMNH). It was found in montane steppe and forest, living among "stones in mt. [montane] gull[ies]" (*ibid.*). Although its status is uncertain, it is likely that it is severely endangered. Control of vertebrate pests in its reported range could be responsible for its rarity. *O. a. nitida* is similarly

isolated and may be at risk, pending surveys of its population size and range.

A distinct form of alpine pika (as yet unnamed) has been found in the Bajan Ulan Mountains on the shore of the Kerulin River (47°N; 109°E) in the Mongolian People's Republic (N. A. Formozov, unpublished data). Its status is unknown. Other isolated populations of alpine pika occur on separate mountains in the Gobi Desert (e.g. Ikhe Bogdo Ula, 45°N, 100°20'E; Adj Bogdo Ula, 44°50'N, 95°E). They are vulnerable but currently not endangered.

Other subspecies of the alpine pika appear to be common throughout the geographic range of the species.

Description

This is generally a large pika, although some of the subspecies are relatively small. The summer fur varies significantly in different subspecies. The general color of the back is dull, yellowish, ochre-gray darkened by black or dark brown hair tips. The flanks have a rust-red tinge and the ventral surface is pale yellowish ochre. In winter the alpine pika tends toward a gray pelage with a yellowish tinge. The skull is stoutly built, but long and narrow. The incisive foramina are small and rounded; the anterior palatal foramina are completely separate from the incisive. No fenestrae are present in the frontals. In comparison with the northern pika the skull of the alpine pika is longer and less rounded, the orbits are more elongate and the rostrum is markedly longer (Ognev 1940). In addition, the bullae of the alpine pika are relatively narrower and deeper and the rear of the cranium is more strongly flexed downward. In the zone of sympatry, adult alpine pikas are consistently larger in a number of measurements than are northern pikas and are usually less brightly colored, although there is much seasonal and geographic variation.

Distribution

In mountainous areas bordering the Gobi Desert on the north (Altai, Sayan, Khangai, etc.) and from the south and east of Lake Baikal eastward to the upper Amur River drainage (Kazakh SSR, RSFSR, Soviet Union; Mongolian People's Republic; northern Xinjiang, China). An isolated population occurs in the Helan Shan (northwest Ningxia-Hexizoulang-Gansu border, China). (See Fig. 3.1).

Habitat

The preferred habitat is rock and talus (Ognev 1940, Khmelevskaya 1961, Naumov 1974, Wang and Yang 1983, Ma et al. 1987). It may occur in old moss-covered scree or in burrows under tree roots (Ognev 1940, Khmelevskaya 1961). Naumov (1974) reported that alpine pikas are not found in extensive talus devoid of vegetation or in swampy montane tundra.

Alpine and northern pikas partially segregate altitudinally or by microhabitat in their zone of sympatry. Due to competition for shelter, the alpine pika tends to occupy talus with larger stones. In the Khangai Mountains, it lives both above and below northern pikas; in Tuva the latter live at higher elevations than does the alpine pika.

The subspecies *O. alpina argentata* occupies rocky areas in steppe and forest-steppe zones in the Helan Shan mountains; in this region it does not extend up into the alpine zone (Ma Y., personal communication).

Ecology

Average annual mortality rates determined by Orlov and Makushin (1984) differed between populations living in forests (53%) and in the alpine zone (41%); most animals were one to three years of age. In most populations the magnitude of annual fluctuations in density is not significantly different.

An unusual catastrophic drop in pika density occurred throughout the western Sayan Mountains in the early 1970's. Throughout much of this area (extending from 90°00' to 93°30' E) density declined by more than an order of magnitude (Khlebnikova 1978; R. L. Naumov, personal communication). The reasons for such a significant drop in the number of pikas are not clear. Khlebnikov (1977) suggested that an epidemic was responsible, but it is difficult to understand how such a factor could have affected a vast territory simultaneously. A contributing factor to the reduction in pika density was that when the numbers became low, the remaining population was preyed on heavily by sables *Martes zibellina* (Khlebnikov 1977). As of 1986/1987 some localities which had high densities 16 to 17 years earlier were now devoid of pikas (Khlebnikova and Khlebnikov, in press). Apparently the low reproductive rate and insular structure of the habitat of alpine pikas account for this phenomenon.

Alpine pikas, along with northern pikas, can play a very important role in the ecosystem as basic food for sables (Khlebnikov 1977). In the western Sayan Mountains pikas comprise up to 87% of the contents of sable scats (Sokolov 1965). The density of sables is ten times higher in areas with pikas (Khlebnikov 1977). In the Altai Mountains in Kazakh SSR, alpine pikas comprise up to 60% of the diet of sables (Sludski et al. 1982), whereas in the central Altai Mountains sables rarely eat pikas, concentrating instead on the constant harvests of pine nuts from *Pinus sibiricus*.

Alpine pikas follow the typical pika behavior of storing food in large caches (Ognev 1940, Khmelevskaya 1961, Travina 1984). Travina (1984) estimated that up to 30kg/ha of vegetation are stored by pikas when their density approximates ten to twelve individuals per ha. Several ungulate species alter their local distribution in response to these pika stores. In winters with especially heavy snows, Siberian wapiti *Cervus elaphus sibiricus* tend to group in pika habitats. They move through the deep snow from one haypile to another eating the hay. During snowstorms reindeer *Rangifer tarandus* go down from their alpine habitats into the forest to eat the stores of pikas. Domestic cows and horses may feed on pika stores in winter (Melnikov 1974). The density of voles *Clethrionomys* and shrews *Sorex* is four times higher in areas of pika haypiles than in the surrounding forest (Naumov 1974).

Khlebnikova (1978) documented that the alpine pika significantly influences the composition and diversity of the plant community where it occurs. Presence of pikas decreases the proportion of flowering plants, decreases the store of seeds in

the soil and slows down succession of the plant community by eating young trees (including *Pinus sibiricus*, the most important element in the Siberian taiga ecosystem) (Khlebnikov and Shtilmark 1965, Loskutov 1966). On the other hand, the organic remains of pika haypiles stored on talus may facilitate plant colonization on this habitat and the large accumulation of pika pellets under pika shelters gives rise to spots of nitrophilic vegetation (Travina 1984).

Behavior

Alpine pikas live in families composed of an adult pair and their young, depending on season (Khmelevskaya 1961, Khlebnikova 1978). Adult partners share mutual shelters and haypiles within the family feeding territories. The borders of the family feeding territories do not overlap and are relatively stable from one year to the next (Khlebnikova 1978), although home ranges of family groups are more extensive than feeding territories and do overlap.

Like all Eurasian species, and in contrast with North American pikas, the alpine pika has a gland located on its neck, but no cheek (apocrine) gland. Males and females mark corners of stones located primarily near the center of their mutual home range by rubbing with their neck glands. This marking has been observed from April to December, but the best developed glands have been found in males in spring (Sludski et al. 1980, Orlov 1983).

Another specific gland of the alpine pika is the anal gland (Schaffer 1940). The mass of these glands is greater in males than in females and it is also larger during August when haypiles are being constructed than in spring (Sludski et al. 1980).

The long call or "song" of the male is the most complicated and ritualized demonstration of alpine pika vocalizations. It consists of three series of different calls given one after the other. Males respond to playbacks of this song with the same song. This type of long call is characteristic of the subspecies *O. a. alpina*, *O. a. nitida* and *O. a. changaica*, but has not been heard from *O. a. cinereofusca* and *O. a. scorodumovi* (N. A. Formozov, unpublished data; V. M. Smirin, personal communication). The short call (except for *O. a. spp.* from the Bajan Ulan Mountains) is a strident sharp whistle that is easily distinguished from the very short and high-pitched whistle of the sympatric northern pika (Formozov and Nikolski 1979, Nikolski 1983, Formozov and Yakhontov 1988). Alpine pikas also vocalize during chases with conspecifics. Alarm calls are uttered immediately upon perception of any cause for alarm (predators, approach of persons, etc.). They perceive danger and respond with alarm calls over a greater distance than most pika species (Oko and Formozov 1980).

This pika adapts very easily to life in captivity (V. M. Smirin, personal communication).

Reproduction

Fecundity is low and characteristic of other talus-dwelling pikas. Litter size varies seasonally and number of litters per season decreases with increasing elevation (Smirnov 1967). In the western Altai, the alpine pika has two litters: the first, $\bar{x} =$

3.0 (2-4; N = 12); the second, $\bar{x}$ = 4.4 (3-6; N = 8) (Sludski et al. 1980). Potapkina (1975) also recorded a seasonal increase in litter size: April, $\bar{x}$ = 2.5; May, $\bar{x}$ = 3.2; June, $\bar{x}$ = 3.6. In the northwestern Altai, the alpine pika has no fewer than two litters with a mean size of 2.7 (1-5; N = 23) (Khmelevskaya 1960). In the western Sayan Mountains mean litter size is 2.7 (1-4; N = 55). Here 10% of females were observed to conceive a third litter (Naumov 1974). Naumov's (1974) observation that some yearling females may breed has not been confirmed by any subsequent investigations.

Gansu or Gray Pika *Ochotona cansus* Lyon 1907

Subspecies: *Ochotona cansus cansus* Lyon 1907; *Ochotona cansus morosa* Thomas 1912a; *Ochotona cansus sorella* Thomas 1908a, 1908b; *Ochotona cansus stevensi* Osgood 1932

Taxonomy

Büchner (1890) originally included the Gansu pika *O. cansus* in Royle's pika *O. roylei*, but it is quite unlike that species. It frequently has been included in *O. thibetana* (Allen 1938, Argyropulo 1948, Ellerman and Morrison-Scott 1951, Gureev

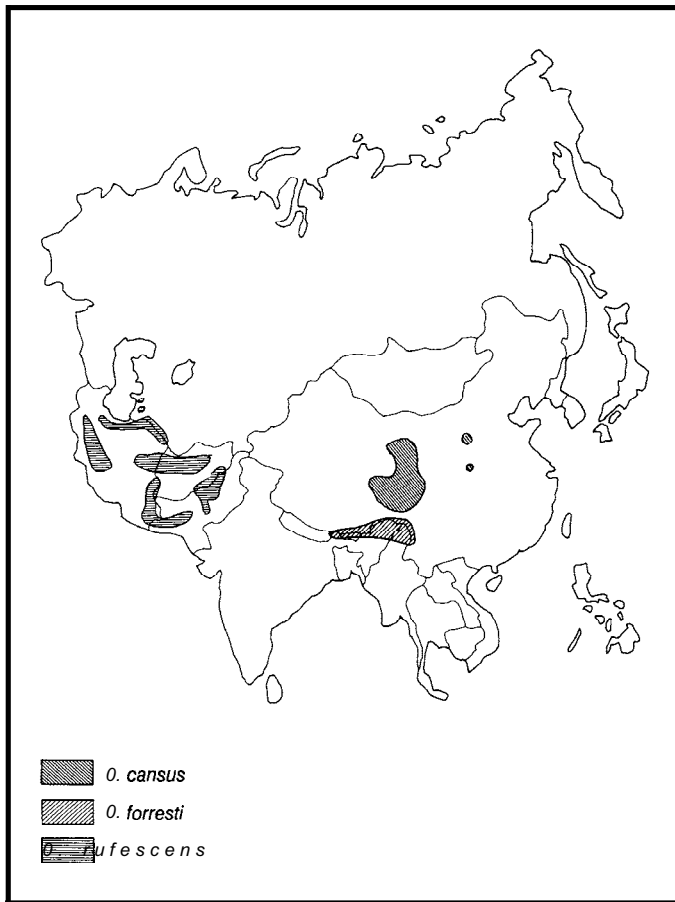


Figure 3.2 Distribution of Gansu pika *Ochotona cansus* Forrest's pika *Ochotona forresti* and Afghan pika *Ochotona rufescens* in Asia

1964, Corbet 1978, Honacki, Kinman and Koepl 1982, Weston 1982). Although morphologically similar to Moupin pika *O. thibetana*, the Gansu pika is here considered an independent species on the basis of its skull characteristics and the observation that intermediate forms are not found in the extensive zone of sympatry between the two species (Feng and Kao 1974, Feng and Zheng 1985). Compared with the Moupin pika, the Gansu pika has a shorter skull, narrower zygomatic arch and narrower interorbital width. Although Weston (1982) included *O. cansus* in *thibetana*, her morphometric analysis clearly shows the distinctiveness of the two forms.

Allen (1938) and Feng and Kao (1974) considered the form *morosa* to be a synonym of *O. thibetana huangensis*, with which it is sympatric in the Tsing Ling Shan of Shaanxi Province, China. However, the describer of *morosa* placed it as a subspecies of the Gansu pika (Thomas 1912a), as did Osgood (1932). The holotype of *morosa* (BMNH) and a series of three additional specimens (American Museum of Natural History, New York: AMNH) from the type locality all display the smaller size, narrower zygomatic and interorbital width, and pelage color typical of *cansus*. Feng and Kao (1974) also assigned to *O. c. cansus* the race *sikimaria*, which we believe belongs in Moupin pika *O. thibetana*, as did Osgood (1932) (see that account). The last subspecies of *cansus* to be named was *stevensi*, by Osgood (1932). Examination of the holotype and a large type series (Field Museum of Natural History, Chicago: FMNH) indicates that they are all correctly placed in the Gansu pika *O. cansus*. Specimens of *O. c. stevensi* are also known from the same places that the Moupin pika occurs (Minya Konka, Sichuan, China).

The most isolated form geographically of the Gansu pika is *sorella*, which is restricted to the Yunzhong Shan in Shanxi Province between the cities of Ningwu and Taiyuan, China. It was originally described as a species "allied to *O. cansus*" by Thomas (1908b) and was considered a synonym of *cansus* by Feng and Kao (1974). However, doubt was raised by Allen (1938), who questioned the assertion by Thomas that it was a "very small species," and subsequently assigned it as a subspecies of the Moupin pika *O. thibetana*. One of us (RSH) has examined the holotype (BMNH) and the only other known specimen of *sorella*, and determined that its cranial measurements supports its assignment to *O. cansus*.

Status and Summary

Most populations of alpine pika are fairly abundant and occupy an ecological zone which does not overlap with the activities of domestic herbivores or humans, thus they are not considered a sensitive species. The form *sorella* (range: Ningwu, Shanxi, China), however, is known from only a few specimens and there have been no records for over a half a century. The status of this subspecies may have been affected by the wide-scale and general application of chemicals to control putative pest vertebrates throughout its geographic range. Details of the magnitude, effect and ramifications of these control measures are presented above,

Another isolated population, about which we have very little information, is *O. c. morosa* in the Tsing Ling Shan, Shaanxi, China.

Description

There is considerable variation in summer dorsal pelage coloration throughout the range of the Gansu pika. In general this is a dull-grayish buff animal with a white to buff-white ventral surface and usually a buffy throat and mid-ventral stripe. Winter pelage is uniformly grayish-drab. It is a relatively small pika (generally less than 70g), with a proportionally large skull. The outline of the braincase is pear-shaped.

Distribution

Western Shanxi, southern Shaanxi, southwestern Gansu, eastern and southern Qinghai, northwestern Sichuan, China. (See Fig. 3.2).

Habitat

A characteristic burrowing pika, living in *Dasiphora* [= *Potentilla*] *fruticosa* scrub forests adjoining alpine meadow or in grassy embankments under spruces (Allen 1938, Feng and Kao 1974, Feng, Cai and Zheng 1986). It appears that the

pikas avoid the thickest areas of brush, preferring instead areas that are slightly open such as natural mounds or mounds created by zokors *Myospalax baileyi* (Jiang Y. and Wang Z., unpublished data). Where it occurs sympatrically with the black-lipped pika *O. curzoniae*, the Gansu pika is excluded from open alpine meadows. The elevational range of this species is 2,700 to 3,800m above sea level (Feng and Kao 1974).

Ecology

Male home ranges overlap little with other males, and females also maintain relatively discrete home ranges. There may be considerable overlap between male and female home ranges. Home range size varies seasonally. In spring home ranges of females ($\bar{x} = 520\text{m}^2$) were smaller and more stable than those of males ($\bar{x} = 1,233\text{m}^2$). During summer, and coincident with the presence of juveniles, home ranges of both sexes enlarged (males: $4,001\text{m}^2$; females: $1,056\text{m}^2$). Placement of natal burrows is near the border of home ranges, and it is in these marginal localities that juveniles initially establish. In autumn the rate of mortality increases and a basic rearrangement of individuals may occur. Should paired adults remain alive, they continue their pair bond. Other animals wander until they



The Gansu pika *Ochotona cansus* in native habitat of alpine shrub at the Haibei Alpine Research Station, Qinghai Province, People's Republic of China (Photo by Andrew Smith)

encounter an animal of the opposite sex with which to settle. The spatial organization of individuals established during autumn persists throughout the winter and at this time home ranges contract to their smallest size (males: 772m²; females: 459m²). Overlap between paired males and females is high (66%) and they share the same burrow system (Jiang Y. and Wang Z., unpublished data).

The Gansu pika burrow system is one of the least complex of all the pikas. Usually there are only a few openings, several branching tunnels and a single nest chamber. Tunnels are approximately one metre in length (Jiang Y. and Wang Z., unpublished data). Occasionally they may be found living in old burrows of Himalayan marmots *Marmota himalayana* (Feng and Kao 1974).

Behavior

The primary social organization is that of pairs of adults and, during the summer, their young. Upon death or disappearance of a male, however, neighboring males extend their influence to include the home ranges of additional females. This organization implies a basic monogamous mating system coupled with facultative polygyny. Aggression between adult males may occur and generally takes place at the borders of their home ranges. Encounters or behavioral interactions between adult females are rarely observed. Almost all affiliative interactions (mouth-nose rubbing, allogrooming, sitting in contact) occur between paired animals (Jiang Y. and Wang Z., unpublished data).

Four types of calls have been distinguished. The long call is uttered only by males, most frequently during the mating season. Both males and females give short calls and there are no obvious differences between the sexes. Individuals uttering short calls are very alert and wary; they normally give the call while simultaneously hiding in bushes or moving toward their burrow entrance. Conspecifics return the short calls uttered by their neighbors, especially in the case of repeated short calls that signal alarm. Trills are given by both sexes and appear to be a form of intra-family contact; usually pikas in the vicinity of the caller immediately give a similar call in response. Whines are primarily uttered by young juveniles during the weaning period or just following weaning. Whines are usually uttered when the caller is near the entrance to its natal burrow. This call tends to show the uneasy state of young pikas and functions for mother-infant contact (Jiang Y. and Wang Z., unpublished data).

Two types of scent marking are exhibited. Neck-rubbing is performed during the breeding season and primarily occurs in the zones of home range overlap between adult males. Rarely do adults anus-rub. A more general form of olfactory communication appears to be the habit of defecating at specific locations (Jiang Y. and Wang Z., unpublished data).

Several elements of the behavior of the Gansu pika reflect the visually disrupted (shrubby) habitat it occupies. Unlike meadow-dwelling pikas (such as the black-lipped), the Gansu pika seldom enters its burrows throughout the daytime activity period, even when it is windy or raining. The time they



Shrubby habitat of the Gansu pika *Ochotona cansus*: Qinghai Nan Shan, Qinghai Province, People's Republic of China
(Photo by Andrew Smith)

spend in surface activity is twice that of black-lipped pika. The Gansu pika rarely utilizes a bipedal stance that is commonly found in steppe-dwelling pikas. It does not flee toward its burrows until predators approach closely and these pikas frequently emerge from their burrow only a short time (as short as several seconds) following their concealment there from a potential predator (Jiang Y. and Wang Z., unpublished data).

Although the Gansu pika is primarily diurnal, it may also be active at dusk and at night (Büchner 1890; Feng, Cai and Zheng 1986; Zheng 1989).

Reproduction

The breeding season extends from early April until late August. Female estrus is not synchronous within populations. Gestation is approximately 20 days and lactation, 18 days. Young have been seen to emerge from their natal burrow at ten days of age. Two to three litters are born per season (Zheng 1989, Jiang Y. and Wang Z., unpublished data). Females may breed in the year of their birth. Litter sizes range from one to six (Allen 1938, Feng and Kao 1974, Zheng 1989, Jiang Y. and Wang Z. unpublished data).

Maternal care is restricted; mothers often spend only 30 minutes, and as few as ten minutes, per day nursing their young. Males do not contribute directly to care of young (Jiang Y. and Wang Z., unpublished data).

Collared pika

Ochotona collaris (Nelson 1893)

Taxonomy

This monotypic species has been included at various times with the similar American *O. princeps*, northern *O. hyperborea* and alpine *O. alpina* pikas. Broadbooks (1965) and Youngman (1975) considered the collared pika conspecific with the American pika. Argyropulo (1948), Gureev (1964) and

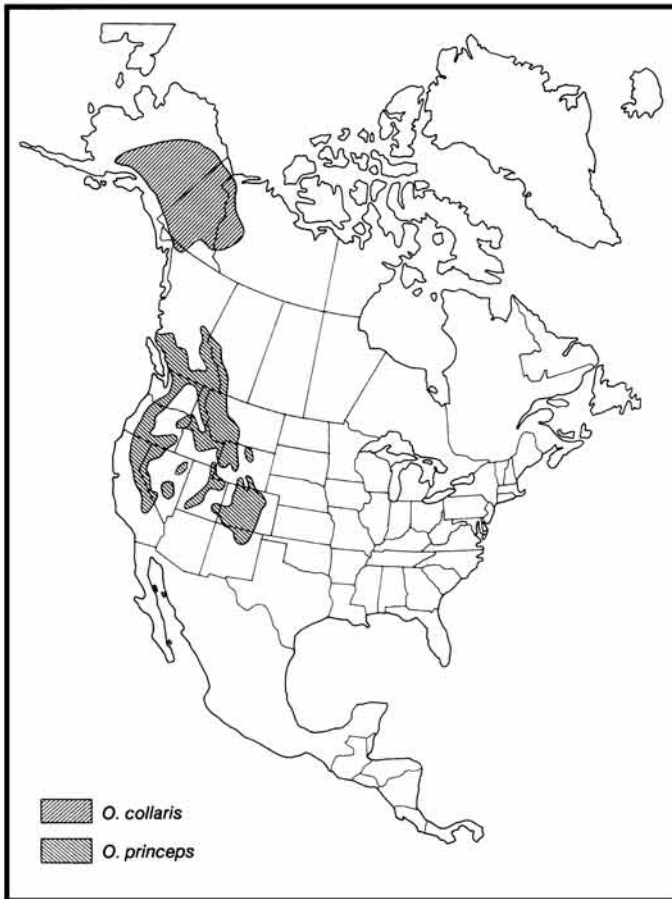


Figure 3.3 Distribution of collared pika *Ochotona collaris* and American pika *Ochotona princeps* in North America

Corbet (1978) treated it under the alpine pika *O. alpina*, along with the American and northern pikas. Weston (1981, 1982) determined that the collared and American pikas are each morphologically distinct from each other and from the Asian forms. Corbet and Hill (1986) treated the four species independently. In addition, the diploid chromosome number of the collared pika is 68 (as is that of the American pika; Hsu and Benirschke 1971), while $2N = 40$ in the northern and 42 in the alpine pikas (Vorontsov and Ivanitskaya 1973).

Status and Summary

The collared pika occupies remote areas and is unlikely to be negatively influenced by humans. All aspects of the systematics and biology of this species have been reviewed recently by MacDonald and Jones (1987)

Description

A medium sized gray pika. Grayish patches on the nape and shoulders form an indistinct collar. Ventral coloration is a creamy white. The skull is relatively broad with a correspondingly broad and flat interorbital region. There are no fenestrae in the frontals.

Distribution

In the mountains of central and southern Alaska, United States and northwestern Canada. (See Fig. 3.3).

Habitat

A typical rock and talus-dwelling pika (Broadbooks 1965).

Ecology

Adult collared pikas occupy individually defended territories on talus, generally at the talus-meadow interface. Average distance between territory centres ranges from 30 to 70m (Broadbooks 1965). Population density ranges from 6.4-7.2 animals/ha (Broadbooks 1965).

Food is stored in caches, typical of most pikas. Although they are generalized herbivores, they evidently are selective of the plants stored in haypiles (Osgood 1909, Rausch 1962). Occasionally the scats of marmots *Marmota caligata* and weasels *Mustela erminea* have been noted on haypiles (Rausch 1962, Broadbooks 1965). Haypiles tend to be constructed in the same places year after year (Broadbooks 1965).

Behavior

The social behavior of the collared pika has not been investigated in detail. Preliminary data indicate that the social system is similar to that described for the American pika (Smith 1981a).

The collared pika is vocal, with short calls given by both sexes and all ages (Broadbooks 1965, Kawamichi 1981). The chattering long call, characteristically uttered by male American pikas and most Asian pikas, is lacking, but males do give strong successive calls during the reproductive season (Kawamichi 1981) and these apparently play the role of long calls in other pikas.

Reproduction

Typical of talus-dwelling pikas, the collared pika has a low fecundity rate. Litter size averages 2.2 (R. P. Hobbs, personal communication) to three (Rausch 1962). Two litters are born per year in a breeding season that commences in May (Rausch 1962, Youngman 1975, R. Smith 1978). Young reproduce first as yearlings (R. Smith 1978).

Black-lipped or Plateau Pika *Ochotona curzoniae* (Hodgson 1858)

Includes *Ochotona melanostoma*

Taxonomy

The black-lipped pika *O. curzoniae* is included in Daurian pika *O. daurica* by Allen (1938, the form *melanostoma* only) and Ellerman and Morrison-Scott (1951), but most authors recognize it as a distinct species (Argyropulo 1948, Gureev 1964, Corbet 1978, Honacki, Kinman and Koeppl 1982, Weston 1982, Feng and Zheng 1985, Feng, Cai and Zheng 1986). The

black-lipped and Daurian pikas occur in sympatry in the Hainan district, Qinghai Province, China (Chang 1983). Zhou and Xia (1981) conducted an electrophoretic survey of serum proteins of these two species and concluded that they were independent. The diploid chromosome number of black-lipped pika *O. curzoniae* ($2N = 46$; Tan and Bai 1987) also differs from that of Daurian pika *O. daurica* ($2N = 50$; Vorontsov and Ivanitskaya 1973).

The form *melanostoma* (Büchner 1890) apparently was described originally without knowledge of *O. curzoniae* (it is compared only with the Daurian pika). Most authors treat *melanostoma* as a synonym of *O. curzoniae* (Gureev 1964, Corbet 1978, Feng and Zheng 1985, Feng, Cai and Zheng 1986) and we agree.

The form *seiana* (from the Iran-Afghanistan border region and disjunct from the main distribution of black-lipped pika) was described by Thomas (1922) as possessing "General characters very like those of true *curzoniae*." Corbet (1978), too, suggested that *seiana* "may also belong" to the black-lipped pika following an examination of the holotype. RSH has also examined the holotype of *seiana* (BMNH), as well as holotypes of other named subspecies of Afghan pika *O. rufescens* (see that account), co- or lectotypes of *O. curzoniae* and *melanostoma* (BMNH) and a large series of Afghan pika in the FMNH and National Museum of Natural History, Washington, D.C. (NMNH). In all essential respects, the unique specimen on which the name *seiana* is based resembles the Afghan pika *O. rufescens rufescens*, and we consider it to be a synonym.

Status and Summary

The black-lipped pika has been the focus of wide-scale control efforts throughout its range (Shi *et al.* 1984, Schaller 1985, Fan *et al.* 1986). Millions of hectares have been defaunated in an effort to eliminate these animals so as to increase vegetation available for domestic livestock (yaks, horses, sheep) (Fan,



Social interactions among black-lipped pika *Ochotona curzoniae* in an alpine meadow habitat near Qinghai Lake, Qinghai Province, People's Republic of China (Photo by Andrew Smith)

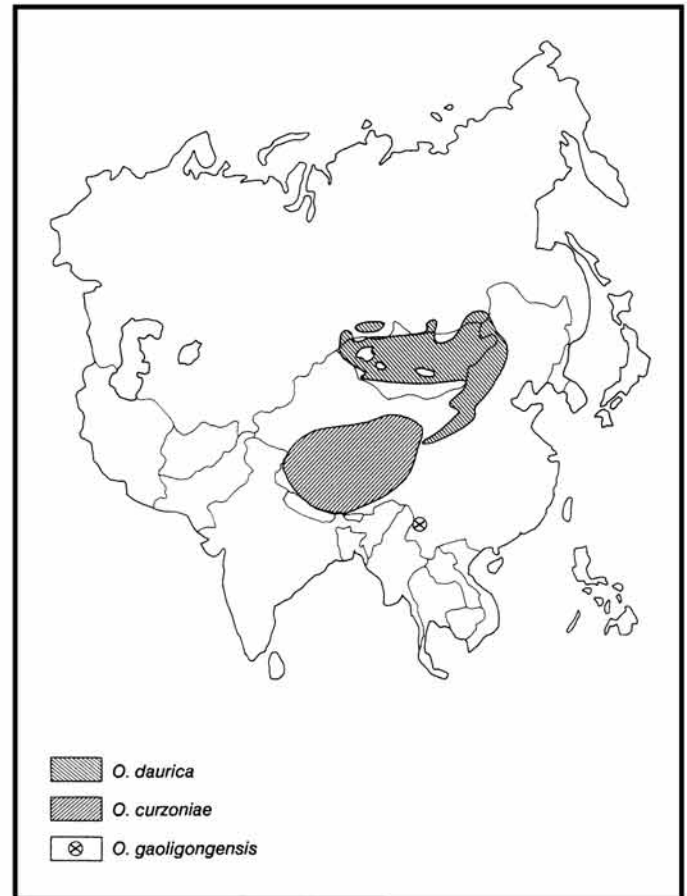


Figure 3.4 Distribution of black-lipped pika *Ochotona curzoniae*, Gaoligong pika *Ochotona gaoligongensis* and Daurian pika *Ochotona daurica* in Asia

personal communication). Details of the magnitude, effect and ramifications of these control measures are presented elsewhere in this volume.

Description

Sandy-brown dorsally and dirty yellowish-white ventrally with a rust-colored patch behind each ear. There is a blackish tip to the nose and the same color extends to the lips as a ring of variable distinctiveness. The skull is of medium size and sharply elevated in the frontal area. The interorbital region is moderately narrow. The tympanic bullae are of moderate size.

Distribution

Southern Xinjiang, Qinghai, Xizang and western Sichuan, China; trans-Himalayan Nepal; and Sikkim, India. (See Fig. 3.4).

Habitat

High alpine desert, steppe and meadows (Liu *et al.* 1982, Shen and Chen 1984, Smith *et al.* 1986a, 1986b)

Ecology

Black-lipped pikas live in family-controlled burrow systems. Normally a burrow system is occupied by a single adult male and adult female and their offspring (monogamy), although various combinations of adult males and females may give rise to polygyny or even polyandry (Liang 1981, Smith *et al.* 1986a, 1986b, Wang and Smith 1988, 1989).

Population density is low in spring following high overwinter mortality. Following the breeding season, the density may approach 380 per ha. Weather during some winters, particularly those with heavy snowfall, may cause catastrophic mortality of these pikas (Zong, Xia and Sun 1986, Wang X.G., personal communication).

The foraging of pikas at low and moderate densities is selective and overlaps little with the diet of domestic grazing animals; thus they may play an important role in the stabilization of the alpine meadow vegetational community (Jiang and Xia 1985, 1987). However, the diet of pikas may overlap extensively with that of domestic animals when their density is extremely high at the end of the breeding season and as availability of food resources declines following the summer growing period. Shi (1983) determined that the black-lipped pika is found at higher densities when the degree of cover and height of vegetation is low (presumably due to grazing of

livestock), and that under these conditions the pikas may further destroy the rangeland. The numerous burrows constructed by pikas have also been implicated in the destruction of the alpine grassland. Dietary overlap with domestic animals and burrow construction by black-lipped pikas are responsible for its label as a pest species in China (Liu, Zhang and Xin 1980, Shen and Chen 1984, Jiang and Xia 1985, 1987). Apparently little consideration has been given to the possibility that overgrazing by domestic animals may be responsible for the degradation of range land, or to the likelihood that the burrowing activity of pikas may play an important role in soil aeration and nutrient cycling. However, Shi (1983) concluded that the most effective way to control damage by pikas is to improve the condition of the range, which presumably would be by controlling grazing intensity.

Schaller (1985) reports that this species stores its cache of vegetation near burrow entrances.

Black-lipped pikas form an important prey base for carnivores throughout their geographic range. They are largely sympatric with the steppe-polecat *Mustela eversmanni*, a species that apparently specializes on pikas. In addition, when Przewalski (1883) secondarily defined *Ursus arctos pruinosus* from Tibet, he called it *U. lagomyiarius*, or bear pika-eater. Kozlov (1899) found 25 pikas in the stomach of one bear.



Wet season habitat (alpine meadow) of the black-lipped pika *O. curzoniae* near Qinghai Lake, Qinghai Province, People's Republic of China (Photo by Andrew Smith)

Behavior

The black-lipped pika is a highly social species; almost 10% of the time individuals spend active on the surface during the summer breeding season is spent in a social context (Smith *et al.* 1986a, 1986b). The expression of most of these behaviors appears independent of age or sex (Smith *et al.* 1986a, 1986b, Smith 1988). Most of the behaviors are affiliative and are expressed among the members of a family burrow system. Aggressive behaviors usually occur between individuals who occupy different family burrow systems. This species also exhibits a rich vocal repertoire and most of the distinctive calls are uttered in a social context (Smith *et al.* 1986a, 1986b). Young from sequential litters occupy a family burrow system with their parents for up to one year. Dispersal during this time is infrequent. Most dispersal is by males and occurs just prior to the breeding season; most males move only one burrow system away from their natal site (Wang X.G. and A.T. Smith, unpublished data). During the mating season males mate-guard females. Cuckoldry is uncommon and occurs primarily to those polygynous males attempting to guard two or more females. Death of an adult male leads to the takeover of his mate(s) by a neighboring male. In these situations the behavior of the new male toward juveniles in his new burrow system is indistinguishable from that of their father (A.T. Smith and Wang X.G., unpublished data).

Black-lipped pikas are active throughout the day (Feng, Cai and Zheng 1986, A.T. Smith and Wang X.G., unpublished data), although Zheng (1989) reported that they are most active from 08.00 to 10.00 and 17.00 to 19.00 hours.

Reproduction

The reproductive rate is high (Smith 1988). Three to five litters may be produced at three week intervals and litter size tends to increase over the reproductive season. In Qinghai the reproductive season begins in April and may extend until August. Litter size (number of young at weaning) ranges from two to eight (A.T. Smith and Wang X.G., unpublished data).

Daurian Pika

Ochotona daurica (Pallas 1776)

Subspecies: *Ochotona daurica altaiana* Thomas 1911a; *Ochotona daurica annectens* Miller 1911; *Ochotona daurica bedfordi* Thomas 1908a, 1908b; *Ochotona daurica daurica* (Pallas 1776); *Ochotona daurica mursaevi* Bannikov 1951

Taxonomy

The form *melanostoma*, which we assign to black-lipped pika *O. curzoniae*, was tentatively included in Daurian pika *O. daurica* by Allen (1938). Ellerman and Morrison-Scott (1951) included *O. curzoniae* in *O. daurica* along with the forms *melanostoma* and *seiana*. Here *curzoniae* and *daurica* are separated following most recent treatments (Argyropulo 1948, Gureev 1964, Corbet 1978, Honacki, Kinman and Koepl 1982, Weston 1982, Feng and Zheng 1985, Feng, Cai and Zheng 1986). Zhou and Xia (1981) determined that these

two forms were independent species based on an electrophoretic analysis of their serum proteins, and the diploid chromosome number of Daurian pika ($2N = 50$; Vorontsov and Ivanitskaya 1973) differs from that of black-lipped pika ($2N = 46$; Tan and Bai 1987).

Status and Summary

Along with the black-lipped pika, the Daurian pika has been considered a pest species in China and has been the target of wide-scale control efforts (Zhong, Zhou and Sun 1985, Fan, personal communication). Briefly, it was controlled in the Soviet Union. Details of the magnitude, effect and ramifications of these control measures are presented above. Vinogradov and Argyropulo (1941) indicated that the Daurian pika has been a secondary fur animal.

The Daurian pika occurs in isolated localities around the northern and southern edges of the Gobi Desert (Sokolov and Orlov 1980, N.A. Formozov, unpublished data); these isolated populations are very vulnerable.

Description

Summer pelage varies from pale, yellowish straw-gray to duller and deeper straw-gray. The flanks are light with a yellowish tinge and the belly is pure white. Winter pelage differs markedly from summer fur in being significantly longer and lighter. In contrast to the black-lipped pika, there is no rust-colored patch behind each ear. The area surrounding the mouth and the nose itself is whitish to buffy white. The skull is of medium size and is only slightly elevated in the frontal area. No frontal fenestrae are present and the tympanic bullae are large.

Distribution

Desert steppes of the Gobi region throughout Mongolia and adjacent regions of the Soviet Union and China (eastern Qinghai, Gansu, Ningxia, Shanxi, Shaanxi, Nei Mongol, Liaoning, northern Hebei). (See Fig. 3.4).

Habitat

A characteristic semi-desert or steppe-dwelling pika (Vinogradov and Argyropulo 1941, Allen 1938, Loukashkin 1940, Ognev 1940, Zevagmid 1975, Smirnov 1986, Zheng 1989). Ognev (1940) noted that they often settle in damp or low-lying places which may be subject to flooding and that their habitat includes fertile parts of the Gobi Desert.

Ecology

Much of the ecology of the Daurian pika appears similar to the closely related black-lipped pika. Large continuous colonies of pikas are composed of individual burrow systems which may each occupy about 25-35m² with 15-20 exits (Ognev 1940). Individual burrows differ greatly in construction, complexity and the number of entrances. This variation is a function of habitat and age (Schauer 1987b).

Populations fluctuate widely in size (Ognev 1940, Leont'ev 1968, Zevagmid 1975). Density may vary between 0.1 to over 300 per ha (Ognev 1940, Leont'ev 1968). These fluctuations

have been attributed to flooding and to competition with other grazing herbivores, such as *Microtus brandti* and domestic ungulates (Zevegmid 1975). In addition, Nekipelov (1954) stated that natural factors such as snowless winters, summer droughts and rain during the fall (that in turn rots stored vegetation), may cause high mortality in Daurian pikas. In some populations young pikas may make up 93% of the population during the summer (Shubin 1966). The potential for attaining high population densities is the reason they are considered a pest species in China. In the central Khangai, however, yearlings comprise only 35% of the population. In this locality 23% of the population were one-year-old animals; 20%, two-year-old animals; 17%, three-year-old animals; and 4%, four-year-old animals (Tsendzhav 1977). Females comprise 59% of young animals, but the sex ratio changes with age and favors males in the older age classes (Eshchelkin, Lazarev and Prutov 1968, Tsendzhav 1976, 1977).

Daurian pikas are selective herbivores and may store large quantities of vegetation in haystacks at the entrances to their burrows (Loukashkin 1940, Ognev 1940, Nekipelov 1959). Dmitriev (1985) determined that certain steppe shrubs grow only where their burrows are found, indicating the importance of these pikas in the local determination of floral diversity. Tsendzhav (1980a, 1985) determined that digging activity loosened and improved the soil. Burrow systems also concentrate many organic materials. The soil in the burrow system contains more humus, nitrogen, calcium and phosphorus, and is of higher humidity than in nearby areas without burrows (Tsendzhav 1985). As a result of these factors the biomass of roots is greater, plants are taller and plant cover is greater around the burrow systems of Daurian pikas than non-burrow areas. In spring the growth phenology of plants on the burrow system is ten to fifteen days earlier than surrounding areas (Tsendzhav 1985). Tsendzhav (1980b) and Nikolski, Guricheva and Dmitriev (1984) found that the forage preferred and eaten by Daurian pikas was not found in the diet of grazing domestic ungulates. Zhong, Zhou and Sun (1985) showed that Daurian pikas are more likely to contribute to the deterioration of rangeland if it was already overgrazed. They concluded that the most effective manner in which to control the "pest" pikas is to improve all aspects of range management, including the prevention of overgrazing.

The Daurian pika is an important prey of the steppe eagle *Aquila nipalensis*, upland buzzard *Buteo hemilasius*, eagle owl *Bubo bubo* and saker falcon *Falco cherrug* (Peshkov 1957, 1967). Because many steppe mammals hibernate (Formozov 1966), this non-hibernating pika is a very important winter food of the corsac fox *Vulpes corsac* and the steppe polecat *Mustela eversmanni* (Nekipelov 1954).

Behavior

Daurian pikas live in pairs on territories which overlap widely (Ol'kova 1954). Aggressive interactions occur rarely within family groups on a territory, but affiliative behavior is frequently expressed (Proskurina, Formozov and Derviz 1985). The most common social behaviors are grooming, soliciting grooming, following each other, crawling on top of each other

and huddling together; boxing episodes are rare and brief (Proskurina and Smirin 1987).

Adults have three basic vocalizations. The alarm call is a short high whistle. The long call is a song-like trill that slows in frequency toward the end. This call is usually uttered by males, but females may use it occasionally (Smirnov, Snarski and Chetverikova 1987). They also utter short trills that are somewhat like the song, but are shorter and of a different frequency spectrum. Very often these short trills follow a song (N.S. Proskurina, personal communication).

Reproduction

The reproductive rate is high. Litter size ranges from one to eleven (Ognev 1940, Eshchelkin, Lazarev and Prutov 1968, Zevegmid 1975). The period of reproduction is long and each female is capable of producing several litters per year (Formozov 1929, Ognev 1940, Eshchelkin, Lazarev and Prutov 1968). Juveniles may reproduce in the summer in which they were born (Zevgmid 1975).

Red-eared or Chinese Red Pika *Ochotona erythrotis* (Büchner 1890)

Taxonomy

The red-eared pika *O. erythrotis* is treated here as a monotypic form; the form described as *O. erythrotis vulpina* Howell 1928 was considered a synonym by Allen (1938), Argyropulo (1948), Ellerman and Morrison-Scott (1951) and Feng and Zheng (1985). The forms *gloveri* and *brookei* were included in *O. erythrotis* by Gureev (1964), Corbet (1978), Honacki, Kinman and Koepl (1982) and Weston (1982), and most authors comment on the closeness in appearance of the three taxa. Separation of the red-eared pika *O. erythrotis* and Glover's pika *O. gloveri* (including *brookei*) has been made on the basis of their pelage coloration (*erythrotis* has a distinctive reddish mantle compared with *gloveri*) and skull characteristics (*erythrotis* having a larger auditory bullae, shorter nasals and a broader rostrum than *gloveri*) (Thomas 1922, Allen 1938, Argyropulo 1948, Feng and Zheng 1985).

The red-eared pika *O. erythrotis* was included in the Turkistan red pika *O. rutila* by Ellerman and Morrison-Scott (1951). Here *erythrotis* is distinguished from *rutila* on the basis of pelage color, skull morphology and zoogeography (Gureev 1964, Corbet 1978, Honacki, Kinman and Koepl 1982, Weston 1982, Feng and Zheng 1985).

Status and Summary

Insufficient data are available to determine the status of the red-eared pika. As it is found in remote areas and non-agricultural or grazing habitat, populations are unlikely to have been influenced negatively by human activities.

Description

In summer the dorsal pelage has a mantle of bright, uniform rusty red, becoming grayish-rufous posteriorly in some individuals. Ventrally, the chest is reddish and the belly white. In

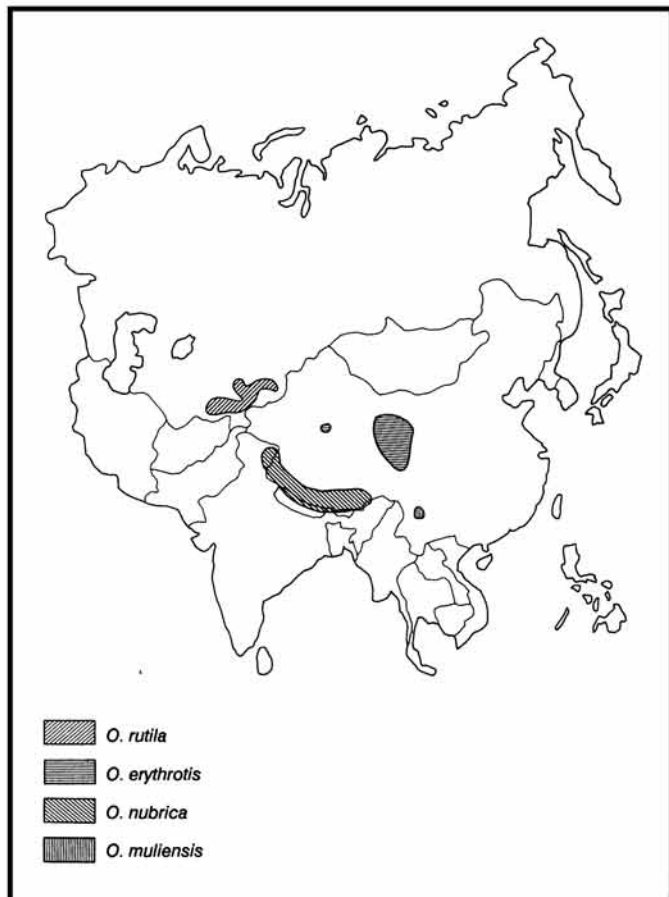


Figure 3.5 Distribution of red-eared pika *Ochotona erythrotis*, Muli pika *O. muliensis*, Nubra pika *O. nubrica* and Turkestan red pika *O. rutila* in Central Asia

winter the species is a drab or pale gray dorsally and ventrally, although the ears retain their reddish coloration. Important aspects of the skull structure distinguishing the red-eared pika from Glover's pika are given above. From the Turkestan red pika it differs in being somewhat smaller, narrower, more arched and in usually possessing frontal fenestrae. Like the Turkestan red pika, this is a comparatively large pika.

Distribution

Occurs at high elevations from the Burchan Budda Mountains of Qinghai to western central Gansu and southern Xinjiang, China. (See Fig. 3.5).

Habitat

Prefers precipitous terrain or cliffs of rock or clay adjoining alpine shrub or meadow habitat (Büchner 1890, Allen 1938), generally at 2,000 to 4,000m elevation (Zheng 1989).

Ecology

Individuals occupy very simple burrows that extend one to two metres in length (Zheng 1989).

Behavior

Przewalski wrote that he never heard the red-eared pika utter any vocalizations (Büchner 1890).

Reproduction

Unknown.

Forrest's Pika

Ochotona forresti Thomas 1923

Taxonomy

This form has generated a high degree of confusion in the already highly confused systematics of *Ochotona*. It has been assigned to the Moupin pika *O. thibetana* (Gureev 1964, Feng and Kao 1974, Honacki, Kinman and Koepl 1982, Weston 1982), to the steppe pika *O. pusilla* (Ellerman and Morrison-Scott 1951) and to Royle's pika *O. roylei* (Corbet 1978). We provisionally consider it a separate species, based on our studies and the assessment of Feng and Zheng (1985) and Feng, Cai and Zheng (1986); see also Allen (1938) and Argypulo (1948). Forrest's pika appears to be allopatric in distribution with Royle's pika and with it may form a superspecies. Other sympatric species include *O. gaoligongensis*, *O. macrotis chinensis*, *O. thibetana sacraria* and *O. gloveri calloceps*.

Status and Summary

The status of Forrest's pika is unknown. However, its restricted distribution suggests that it may be at some risk.

Description

Feng and Zheng (1985) comment on the similarity of Forrest's pika with Moupin pika, but note the following differences between the two species: 1) there is a dark gray area behind each ear and these two areas almost meet across the nape in Forrest's pika, unlike the pale buffy area which does not meet in the Moupin pika; 2) the fore claws are significantly longer in Forrest's pika than in the Moupin pika; 3) the zygomatic arch is wider in Forrest's pika; 4) 70% of Forrest's pika examined had "violin-shaped" confluence of the incisive and palatal foramina due to abrupt constriction of the sides, whereas this constriction is not found in the Moupin pika; and 5) the rectangular shaped posterior end of the nasals are broader in Forrest's pika than the Moupin pika. The coloration of the summer fur is fairly dark reddish, both dorsal and ventrally. In winter, dorsal pelage is dark gray-brown, only slightly lighter ventrally.

Distribution

Northwest Yunnan, southeast Xizang, China; northern Burma; Assam, Sikkim, India; Bhutan. (See Fig. 3.2).

Habitat

Forrest's pika inhabits mountain slopes that face toward the sun at elevations of 2,600 to 4,400m in the forest belt (Feng, Cai and Zheng 1986).

Ecology, Behavior and Reproduction

Unknown.

Gaoligong Pika

Ochotona gaoligongensis Wang, Gong and Duan 1988

Taxonomy

This monotypic species was recently described and has not been included in any prior revisions of the genus. It is **sympatric** with Forrest's pika *O. forresti* and Moupin pika *O. tibetana* on Mount Gaoligong, Yunnan Province, PRC. Wang, Gong and Duan (1988) claim that it is distinctly different from these forms, although they have not compared it with any of the type material. The original description suggests that it should be compared with additional material of *O. forresti*.

Status and Summary

Status is unknown, although Gaoligong pikas may be considered rare on the basis of preliminary investigations. The cause of rareness is unlikely to be due to human influence because of the inaccessible habitat occupied.

Description

The Gaoligong pika is similar to Forrest's pika in size and main characters of the skull. It is distinguished from the latter chiefly by coloration (its head and neck are a brilliant **rufous-brown** and its back a dull rufous-black), by its flattened skull profile, by nasal bones that are longer and with a broader posterior, and by broader condylar processes of the mandibles.

Distribution

Mount Gaoligong, northwest Yunnan Province, China. (See Fig. 3.4).

Habitat

Talus and rocky habitat in forested areas at about 2,950m elevation.

Ecology, Behavior and Reproduction

Unknown.

Glover's Pika

Ochotona gloveri Thomas 1922

Subspecies: *Ochotona gloveri brookei* Allen 1937 (includes *kamensis*); *Ochotona gloveri calloceps* Pen et al. 1962; *Ochotona gloveri gloveri* Thomas 1922

Taxonomy

The forms *gloveri* and *brookei* were included in the Turkestan red pika *O. rutila* (along with the red-eared pika *O. erythrotis*) by Ellerman and Morrison-Scott (1951). Glover's pika has also been placed in *O. erythrotis* (Gureev 1964, Corbet 1978,

Honacki, Kinman and Koepl 1982, Weston 1982) and this association has, in part, been responsible for its listing with *rutila*. The separation of Glover's and red-eared pikas from the Turkestan red pika *O. rutila* has been on the basis of pelage color, skull morphology and zoogeography (see accounts of those species) (Gureev 1964, Weston 1982, Feng and Zheng 1985, Feng, Cai and Zheng 1986).

Glover's pika is probably closely related to the red-eared pika, a point made by even those authors who have separated the forms (Thomas 1922, Allen 1938, Argyropulo 1948, Feng and Zheng 1985, Feng, Cai and Zheng 1986). Distinguishing features are summer pelage (*gloveri* does not possess the reddish mantle of *erythrotis*) and skull morphology (*gloveri* has smaller auditory bullae, more elongate nasals and a more slender rostrum than *erythrotis*) (Thomas 1922, Allen 1938, Argyropulo 1948, Feng and Zheng 1985).

The species described as *O. kamensis* (Argyropulo 1948, see also Gureev 1964, Corbet 1978, Honacki, Kinman and Koepl 1982, Weston 1982) was synonymised with *O. gloveri* by Feng and Zheng (1985). Erbajeva (1988) synonymised *kamensis* with *O. gloveri brookei*, although she did not use the rule of priority and retained the name *kamensis*. In his original description, Argyropulo (1948) comments that *kamensis* is the "largest and most differentiated species in

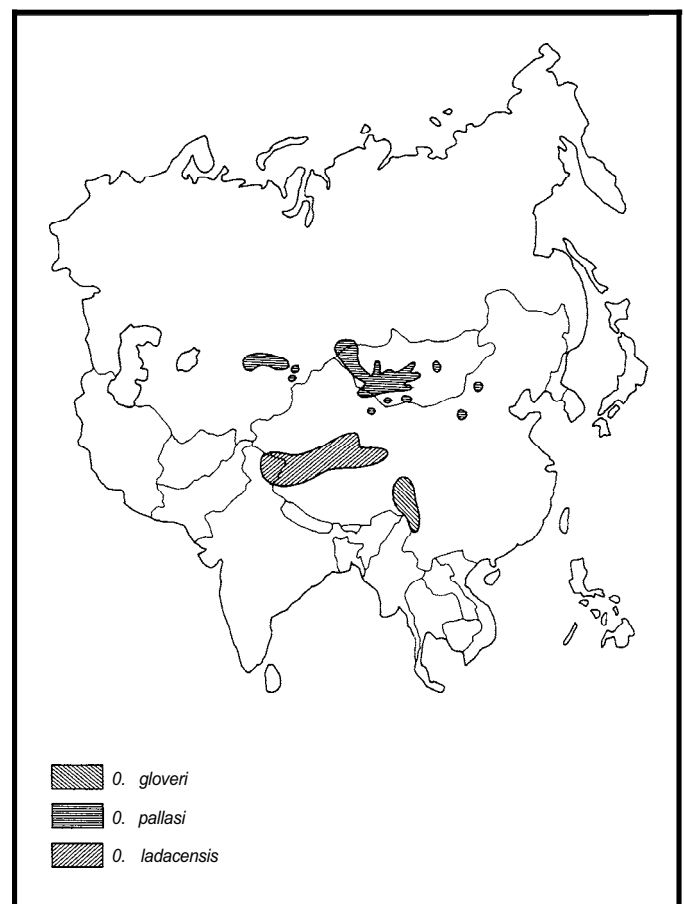


Figure 3.6 Distribution of Glover's pika *Ochotona gloveri*, Pallas's pika *O. pallasi* and Ladak pika *O. ladacensis* in Central Asia

this group [*viz. kamensis, eythrotis* and *gloveri*].” Feng and Zheng (1985), however, noted close similarities between *gloveri* and *kamensis* in coat color and skull structure, and we agree. In addition, the known range of *kamensis* falls within that of *gloveri* (Corbet 1978, Feng and Zheng 1985, Feng, Cai and Zheng 1986). We believe that *kamensis* should be placed in synonymy with *O. gloveri brookei* based on the close proximity of the two type localities (*kamensis*: 32°15'N; 96°40'E; Kozlov 1947; *brookei*: 33°00'N; 96°40'E).

Pen et al. (1962) described a new form as *O. gloveri muliensis*, but now this form is considered a distinct species (Feng and Zheng 1985) on the basis of skull morphology (see *O. muliensis*, the Muli pika).

Status and Summary

Insufficient data are available to determine the status of Glover's pika. As it is found in remote areas and does not occur on agricultural or grazing habitat, populations are unlikely to have been influenced negatively by human activities.

Description

Allen (1938) calls Glover's pika “a smaller darker edition of [the red-eared pika] *O. eythrotis*.” The dorsal coloration in summer is a brownish gray. The ears are brilliant rust or chestnut colored on the back and sparsely clothed with short ferruginous hairs on the inner side. The muzzle and forehead are tinged with dull fulvous, but the cheek area is gray. The ventral coloration is nearly uniform dull whitish. Winter pelage is similar to that found in summer. Important aspects of the skull structure are given above.

Distribution

Occurs at high elevations in southwest Qinghai, northeast Xizang, northwest Yunnan and western Sichuan, China. (See Fig. 3.6).

Habitat

Glover's pika lives in talus, which throughout most of its geographic range is bordered by forest (Feng, Cai and Zheng 1986, Zheng 1989).

Ecology, Behavior and Reproduction

Unknown.

Himalayan Pika *Ochotona himalayana* Feng 1973

Taxonomy

The Himalayan pika *O. himalayana* was synonymised with Royle's pika *O. r. roylei* by Corbet (1978), Honacki, Kinman and Koeppel (1982) and Weston (1982), but is treated as an independent species here following its original description and the analyses of Feng and Zheng (1985) and Feng, Cai and Zheng (1986). However, its range is within that of *O. roylei nepalensis* and additional specimens and field studies are

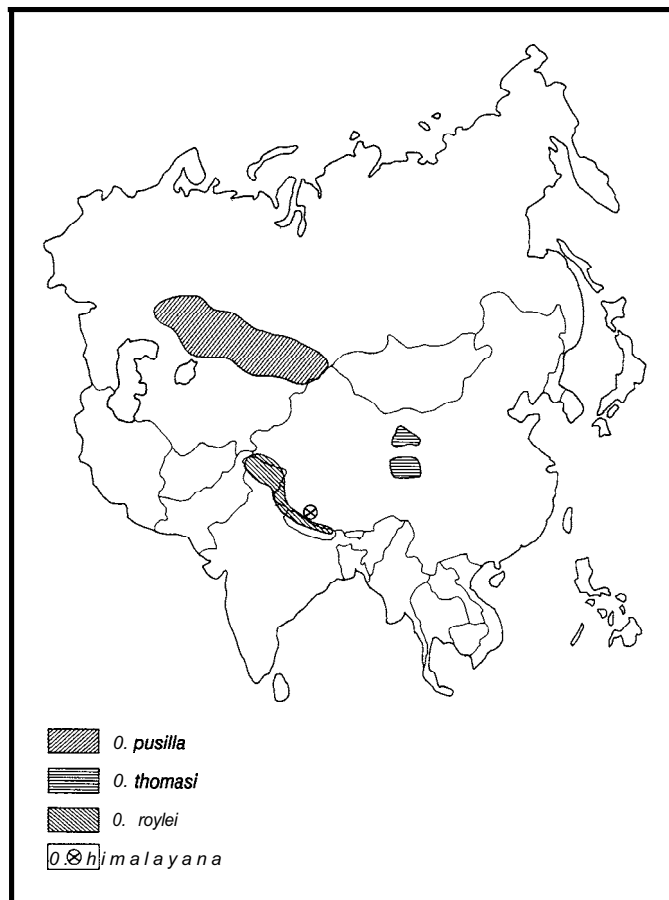


Figure 3.7 Distribution of steppe pika *Ochotona pusilla*, Thomas's pika *O. thomasi* and Royle's pika *O. roylei* and Himalayan pika *O. himalayana* in Central Asia

necessary to confirm its specific distinctness, or to place it within Royle's pika *O. roylei*, which it most closely resembles. Most importantly, attention should be given to the main character used to separate *himalayana* and *roylei*: the lack of foraminae on the frontals. This characteristic is quite variable in most pikas; the presence of these foraminae varies among individuals of the large-eared pika *O. macrotis* and Royle's pika (Zimina 1962, Gruber 1969, Mitchell 1978). The Turkestan red pika *O. rutila* is extremely variable for this character throughout Kirgizia (Yanushevich et al. 1972) and Tadzhikistan (E. Eu. Ivanitskaya, personal communication). Thus although we provisionally keep the species status of the Himalayan pika *O. himalayana*, we note at the same time that *O. mitchelli* and *O. angdawai* are listed as synonyms for Royle's pika, but these two taxa have two pairs of frontal foraminae, unlike typical *roylei*.

Status and Summary

The status of the Himalayan pika is unknown.

Description

The Himalayan pika is a fairly large species and the distinctive elements of its coloration include the rufous or brownish tint

to the head and shoulders. The dorsal surface is a dull grayish brown. The palatal and incisive foramina are completely confluent and there are no foramina on the anterior end of the frontal.

Distribution

Mount Jolmolungma (Everest) area, southern Xizang, China. (See Fig. 3.7).

Habitat

Rocky habitats (such as cracks in walls, precipices, talus and highway scree) bordered by evergreen or broadleaf forests. Elevational range from 2,400 to 4,200m (Feng, Cai and Zheng 1986).

Ecology

Unknown.

Behavior

There are two activity periods: in the morning from 08.00 to 09.00 and at dusk.

Reproduction

Litter size ranges from three to four (Feng, Cai and Zheng 1986).

Northern or Siberian Pika *Ochotona hyperborea* (Pallas 1811)

Subspecies: *Ochotona hyperborea cinereoflava* (Schrenck 1858); *Ochotona hyperborea coreana* Allen and Andrews 1913; *Ochotona hyperborea feminea* (Schrenck 1858) (includes *normalis*, *kamtschaticus*); *Ochotona hyperborea kolymensis* Allen 1903; *Ochotona hyperborea hyperborea* (Pallas 1811) (includes *litoralis*); *Ochotona hyperborea mantchurica* Thomas 1909; *Ochotona hyperborea svatoshi* Turov 1924; *Ochotona hyperborea turuchanensis* Naumov 1934; *Ochotona hyperborea uralensis* Flerov 1927; *Ochotona hyperborea yesoensis* Kishida 1930; *Ochotona hyperborea yoshikurai* Kishida 1932

Taxonomy

The northern pika *O. hyperborea* has been included in the alpine pika *O. alpina* by several authorities (Vinogradov and Argyropulo 1941, Argyropulo 1948, Gureev 1964, Corbet 1978, Honacki, Kinman and Koepl 1982, Weston 1982, Feng and Zheng 1985). Argyropulo (1948), Gureev (1964) and Corbet (1978) also include the North American forms, the American *O. princeps* and collared *O. collaris* pikas with *hyperborea* in the alpine pika *O. alpina*. Here these four forms are treated as separate species. Weston (1981) determined that the North American forms are significantly different morphologically from the Asian forms. Authorities who have had the opportunity to investigate closely northern and alpine

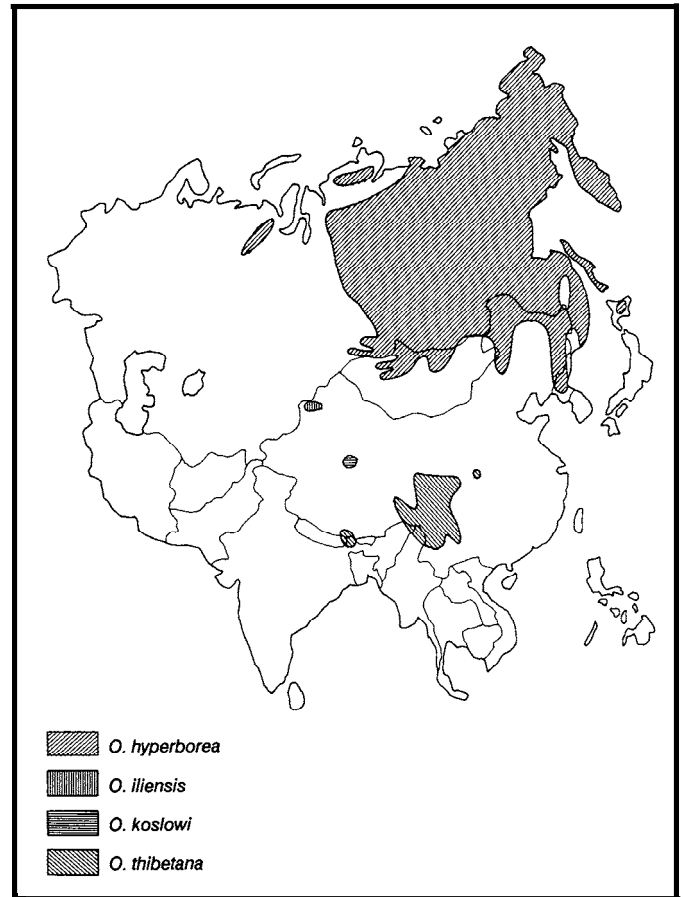


Figure 3.8 Distribution of northern pika *Ochotona hyperborea*, Ili pika *O. iliensis*, Kozlov's pika *O. koslowi* and Moupin pika *O. thibetana* in Asia

pikas comment on their noticeable differences throughout their zone of sympatry (Ognev 1940, Sokolov and Orlov 1980). In addition, the diploid chromosome number is 40 in *O. hyperborea* and 42 in *O. alpina* (Vorontsov and Ivanitskaya 1973). Corbet and Hill (1986) separated the four species.

The assignment of subspecies to the northern pika *O. hyperborea* followed here was based on the form having been included in *hyperborea* by one or more of those authorities who distinguished between the northern and alpine pika species: Ognev (1940), Bobrinski, Kuznetsov and Kuzyakin (1944), Ellerman and Morrison-Scott (1951). In addition, one of us (RSH) has examined specimens of all named subspecies except *cinereoflava*, *uralensis* and *yoshikurai*. Formozov and Nikolski (1979) argued that the form *svatoshi* should be transferred to *O. hyperborea*, and we agree. The forms *kolymensis* and *turuchanensis* were included as subspecies following the recent revisions by Cherniavski (1984) and Yakhontov (1987). *O. h. turuchanensis* was artificially united with *O. h. feminea* by Ognev (1940). These two forms have separate ranges far removed from one another. In addition, *turuchanensis* is considerably larger than *feminea*.

O. hyperborea normalis is usually listed as a synonym of *O. hyperborea hyperborea* (Ellerman and Morrison-Scott 1951).

In fact, it was described by Schrenck (1858) on the basis of one specimen from the “Khalazansk Mountains” (inner parts of south Kamchatka), the same place where the two syntypes of *O. h. ferruginea* were found. All three specimens were collected by I. G. Voznesenski at the same time. Based on the drawing of the specimen, *normalis* was a **subadult** molting into adult fur (Schrenck 1858). There are descriptions of *normalis* and *ferruginea* on the same page, but *normalis* is mentioned first. Formally, pikas from Kamchatka might be called *O. hyperborea normalis*, but for reasons of stability of nomenclature we keep the name *ferruginea* for Kamchatka pikas.

Overall, the northern pika is a very polymorphic species, and its variability has not been adequately studied. Some systematic refinements might be made on the basis of the variation in alarm vocalizations of these pikas. Four dialects have been found (Formozov and Nikolski 1979, Nikolski 1983, Formozov and Yakhontov 1988). Some subspecies, for example *O. h. mantchurica*, probably are composite as they include three different dialect forms. Also, *O. hyperborea* from the Soviet Far East are usually placed in *mantchurica*, yet these animals have calls identical to those of *fyesoensis* from Hokkaido Island, Japan (Kawamichi 1981, Formozov and Yakhontov 1988).

The systematic status of these dialect forms of the northern pika is not clear. For example, there is a variable population in the Putorana Mountains south of the Taimyr Peninsula (92°40'N, 69°10'E). Cluster analysis of 12 cranial measurements indicates three separate groups in the area: two different forms of *O. hyperborea* and intergrades between them. Analysis of the dialects of these forms confirms that there is a secondary contact zone with limited hybridization between the two primary forms (N.A. Formozov and E.L. Yakhontov, unpublished data). However, in the Yana Basin (135°30'N, 67°55'E), all calls are intermediate between the same two dialect forms. This population could be interpreted as being secondarily stabilized after complete introgression (Formozov and Emelianova, in press).

Another aspect of the geographical variability of this species is the character displacement of its size where it is sympatric with *O. alpina*. The northern pika becomes smaller the closer it is to that part of its range where it is sympatric with the alpine pika. For example, northern pikas in the Bulnai Nuro Mountains, MPR (98°00'N, 49°05'E), where there are no alpine pikas, are larger than where found in sympatry with alpine pikas both to the north and south.

Status and Summary

The northern pika appears common throughout its wide geographic range; there is no apparent threat to this form. The subspecies *O. h. yesoensis* has been considered a forest pest and controlled on the island of Hokkaido (Inukai and Shimakura 1930). Prior to World War II, the fur of northern pika was used to produce high quality felt. In Yakutia, the trapping of this species continued until 1953, and in some years as many as 14,000 specimens were caught (Tavrovski *et al.* 1971). Now this activity has largely ceased.

Description

The northern pika is in general smaller than the alpine pika, although the southern races *mantchurica*, *coreana* and *yesoensis*, living in areas where the alpine pika does not occur, are larger than average for the species. Color of the fur varies greatly among subspecies. In general, during summer the back is a light brownish-rufous, becoming a more pure rufous along the sides. The underparts are a uniform rufous-white coloration. Winter fur is significantly grayer with a brownish tinge. In comparison with the alpine pika, the skull of the northern pika is shorter and more rounded, the orbits are not as elongate and the rostrum is markedly shorter (Ognev 1940). No fenestrae are present in the frontals. The incisive foramina are completely separated from the anterior palatine foramina, as in the alpine pika. The auditory bullae are relatively wider but flatter than those of *alpina* and the cranium is less flexed posteriorly. In the zone of sympatry, adult alpine pikas are consistently larger in a number of measurements than are northern pikas and usually less brightly colored, although there is much seasonal and geographical variation.

Distribution

Widely distributed, mainly in the montane taiga of boreal Asia. Its northern boundary penetrates the tundra, but in the south it may be found in more xeric situations. It is found in the Soviet Union in the Ural Mountains and from the east bank of the lower and middle Lena River eastward throughout the Chukotsk and Koryak peninsulas, in the Kamchatka Peninsula and on Sakhalin Island, through the upper Lena drainage, Transbaikaliya and the Amur region to the northern mountains of the Mongolian People's Republic, the northeastern provinces of the People's Republic of China (Nei Mongol, Liaoning, Jilin, Heilongjiang), northern Korea and northern Japan (Hokkaido). The northern pika lives on some islands in the Bering Strait (Arakamchechen Island) and the Sea of Okhotsk (Ol'ski Island in the Tauyskaya Guba, Ognev 1940; Great Shantar Island, Krivosheyev 1984). Northern and alpine pikas have parapatric ranges in the western Sayan Mountains. (See Fig. 3.8).

Habitat

Characteristically a rock-dwelling species (Inukai 1931, Allen 1938, Ognev 1940, Haga 1960, Kim 1962, Belyaev 1968, Kawamichi 1969, Zevagmid 1975). The northern pika is more labile in its choice of habitats than the closely related alpine pika. In the northern tundra region, it occupies huge open rock fields and in northern Yakutia, polygonal clefts that appear in the permafrost (Tavrovski *et al.* 1971). Throughout much of its range it occupies rocky terrain in dark coniferous forests laced with mossy banks (Inukai and Shimakura 1930, Ognev 1940, Kim 1962, Kawamichi 1969). It may also burrow under or around tree stumps or fallen logs (Naumov 1934, Loukashkin 1940, Haga 1960, Voronov 1964, Kishchinski 1969, Safronov and Akhremenko 1982).

In zones of sympatry where northern and alpine pikas

compete for shelters, the northern pika's range of habitats is more restricted. On the Tanu-Ola Ridge, Tuva ASSR, it occupies talus composed of small stones higher in the alpine zone than the habitat occupied by the alpine pika. In areas outside of the zone of sympatry, for example the **Khangay** and **Tarbagatay** ridges, Mongolia, the northern pika lives mostly in forested taluses in the forest zone (Formozov and Yakhontov, in preparation).

Ecology

The density of these pikas apparently varies with locality and populations remain relatively constant over time (Kawamichi 1970). Density estimates include **30/ha** on the lower Lena River (Kapitonov 1961), **38/ha** in the Kolyma Highlands (Kishchinski 1969), **40/ha** on the Sokhondo Mountain (A.A. Nikolski, N.A. Formozov and E.B. Srebrodolskaya, unpublished data) and as low as **3.5-2.2/ha** in Japan (Kawamichi 1969, 1970). The usual density appears to be approximately **20/ha**; the high estimates above were either from extremely optimal habitat (A.A. Nikolski, E.B. Srebrodolskaya and N.A. Formozov, unpublished data) or from small patches of talus. Usually there is a higher density on smaller patches of talus. Northern pikas live mostly on the peripheries of larger talus not far from their feeding territories. Thus in estimations of density, it is necessary to consider not only the area of the talus, but also the length of its border. If one does not do this, density estimates may be inflated. Such is the case in reports of **100/ha** (Revin 1968) and **210/ha** (Safronov and Akhremenko 1982). In each of these cases the pikas occupied long narrow ramparts of logs (**4-15m** wide).

The sex-ratio in northern pika populations is **1:1** (Gashev 1971), although in the abnormally dense population studied by Safronov and Akhremenko (1982), males comprised 60% of the population. In mid-winter Safronov and Akhremenko reported that yearlings made up 62% of the population, whereas 28% were one-year-old animals and 8% **two-year-olds**. Belyaev (1968) observed a population that remained constant in size during three years of study and noted that **65-75%** of the population was renewed annually. Stubbe and Chotolchu (1971) determined that the generation turnover was two years; 67% of the population they sampled were young. Gashev (1966) reported that 20% of his sampled population was two to three years old and he has concluded that it is rare for an animal to survive three winters (Gashev 1971). Revin (1968) found that in September yearlings comprised 50% of the population. Adult one-year-old animals made up **40.5%** and adults two years old and older only 9.5% of the population.

Northern pikas store large amounts of vegetation in their **haypiles** (Inukai 1931, Loukashkin 1940, Ognev 1940, **Haga** 1960, Kawamichi 1969). Reindeer *Rangifer tarandus*, snow sheep *Ovis nivicola*, domestic horses and white hares *Lepus timidus* feed on the stores of northern pikas. In early spring *Marmota camtschatica* also may eat the pika's hay (Kapitonov 1961). In an area of dense population on the middle Lena River, there was an inverse relationship between the density

of pikas and that of small rodents; nevertheless, during winter voles were often caught on pika **haypiles** (Safronov and Akhremenko 1982).

Behavior

Male and female adults live in a joint territory in which they are highly sedentary (Kawamichi 1969, 1970). Each individual tends to stay in this **fixed** area for life, resulting in a "lasting spatial mosaic" (Kawamichi 1971b). Even following death of territory occupants and resettlement by other individuals, the territory boundaries tend to remain the same. Males are more likely than females to cross territorial boundaries into areas occupied by neighboring conspecifics. Females ignore each other and do not respond to each other's vocal signals. The male and female exchange calls most of the year and most probably recognize each other's calls, because they do not respond to the calls of other conspecifics. In fall they store hay together in the same places. Body contact between male and female partners is rare; they do not "snuggle" with each other as do Daurian *O. daurica* and black-lipped pikas *O. curzoniae*.

Some variability in the paired social organisation has been observed. In some cases there may be unpaired males or females, or threesomes with one male associated with two females. Threesomes are found only in areas of high density.

In the southern part of the range of northern pikas, young disperse and form couples in the summer of their birth year (Nikolski, Srebrodolskaya and Formozov 1988). In the northern part of their range, in contrast, young from late litters spend the winter with their parents (Kapitonov 1961). In the Ural Mountains, the young not only wintered with their parents, but also constructed mutual stores with them (Gashev 1971).

A crucial point is that the social organization (whether of couples or threesomes) is not associated with the structure of sexual relations. During the breeding season, all males visit no fewer than three females; and each female is visited by several males, sometimes simultaneously. Some males living in couples travel long distances (over 200m) to visit other females.

Vocalizations produced by northern pikas are very loud and sharp (Loukashkin 1940, **Haga** 1960, Kawamichi 1981, Nikolski, Srebrodolskaya and Formozov 1988). Males utter a long call, whereas all individuals irrespective of age and sex produce a short call and a trill (Kawamichi 1981, Nikolski, Srebrodolskaya and Formozov 1988). The long call consists of a chattering sound followed by a sequence of loud sharp whistles. The dynamic spectrum of these calls is individually specific (Nikolski, Srebrodolskaya and Formozov 1988).

As indicated above, the short call is used for communication between paired males and females. In spring it is used only by females, whereas in fall it is given by both sexes. When the short call is used in alarm situations, the series of calls is fewer than in the alpine pika. The spectrum of short calls in northern pikas is very broad and varies geographically (Formozov and Nikolski 1979, Formozov and Yakhontov 1988).

The northern pika marks its home range by rubbing its neck gland on the corners of stones or by leaving urine in other specific places (Gashev 1971, N.A. Formozov, unpublished data). They mark with their neck gland more actively in spring than in fall. In fall, the visit of an intruder into the core of an animal's home range stimulated marking by the host.

There is cleptoparasitism in this species. Males have been observed stealing hay from as many as five conspecifics (A.A. Nikolski, N.A. Formozov and E.B. Srebrodolskaya, unpublished data).

Like alpine pikas, the northern pika adapts easily to humans and can be made a pet (Yu. L. Vigorov, personal communication).

Reproduction

The fecundity rate is low. Most parameters associated with fecundity vary seasonally, annually and geographically. Length of pregnancy is 28 days (Gashev 1971). Females begin to breed in spring at different times over the course of a month (Revin 1968). This asynchrony makes it difficult to determine the number of litters per year and the percent of breeding females. There is a tendency, in the northern part of the geographic range, for northern pikas to have one large litter, and in the southern part of the range to have two litters of smaller size (Revin 1968), but there are many exceptions. Some sources indicate that young first breed as yearlings (Ognev 1940, Kapitonov 1961, Kawamichi 1971, Tavrovski *et al.* 1971, Zevegmid 1975), although others have stated that yearling females are incapable of breeding (Cherniavski 1984).

Litter size ranges from one to nine. In Japan Kawamichi (1971b) found the average litter size to be 3.1 (range 1-5). In the lower Lena River area there is probably one litter with 2-6 young ($\bar{x}$ = 4.8; Kapitonov 1961). The single litter born in the Polar Ural Mountains averages 3.6 in good years but only 2.0 in unfavorable ones. Percentage resorption of embryos varies similarly from 5.5% in good years to 25% in bad years (Gashev 1971). Safronov and Akhremenko (1982) found that the first litter averaged 3.8 (3-6) whereas the second litter was larger ($\bar{x}$ = 5.6; 2-9). All females initiated first litters, whereas only half of the females had second litters. Other reported litter sizes are: $\bar{x}$ = 4.2 (2-6); $\bar{x}$ = 4.8 (3-8) (Cherniavski 1984); $\bar{x}$ = 4.7 (2-7) (Revin *et al.* 1988); $\bar{x}$ = 2.2 (Revin 1968); $\bar{x}$ = 2.1 (1-3) (Voronov 1964); and $\bar{x}$ = 4.2 (2-7) (Sokolov, Shvetsov and Litvinov 1985).

Ili Pika

Ochotona iliensis Li and Ma 1986

Taxonomy

This monotypic species was recently described and has not been included in any previous revisions of the genus. Its relationship with other species of *Ochotona* requires additional study; because of its reddish color, it should be compared with the red-eared pika *O. erythrotis* and Turkestan red pika *O. rutila*.

Status and Summary

The population status of Ili pikas in China is unknown, although they may be considered rare on the basis of preliminary investigations. The cause of rareness is unlikely to be due to human influence because of the inaccessible habitat they occupy. There are reports of a pika being found (but not collected) approximately fifty years ago in the Dzungarski Alatau Mountains (Shnitnikov 1936). It has not been found since that time, although several Soviet scientists have worked extensively in that area (A. K. Fedosenko, E.Yu. Ivanitskaya, N.A. Formozov). The pika was probably *iliensis*, and its demise could be linked to the gradual climatic warming in the area over the last 200 years.

Description

A fairly large pika, with large ears and hind feet. The general color is relatively bright with large rusty-red spots on the forehead and crown, as well as on the side of the neck.

Distribution

The Borohoro Shan, Xinjiang, China. (See Fig. 3.8).

Habitat

Talus areas on high cliff faces at 2,800 to 3,300m in elevation (Li *et al.* 1988).

Ecology, Behavior and Reproduction

Unknown.

Kozlov's Pika

Ochotona kosłowi (Büchner 1894)

Taxonomy

This monotypic species is one of the few *Ochotona* which has generated no confusion (Ellerman and Morrison-Scott 1951, Gureev 1964, Corbet 1978, Honacki, Kinman and Koepl 1982, Weston 1982, Feng and Zheng 1985); it appears to be thoroughly distinctive (so much so that Argyropulo [1948] proposed the subgenus *Tibetolagus* for this species alone). Its closest relative may be the Ladak pika *O. zadacensis*, with which it shares a derived shape of the confluent incisive and palatal foramina.

Status and Summary

The original specimens of Kozlov's pika were collected by Przewalski in 1884. Approximately one hundred years elapsed before they were seen again (Zheng 1986). Due to their limited distribution and apparent rarity, this should be considered a potentially threatened species. It is the only *Ochotona* species scheduled for listing in the forthcoming People's Republic of China "Red Book of Endangered Species." In addition, it is possible that vertebrate control campaigns directed at other species within its range may be exerting an adverse affect on populations of Kozlov's pika.

Description

This large species is uniformly pale whitish buff tinged with vinaceous coloration dorsally, with thickly furred white underparts. The thickness and density of the fur are greater than any other pika. The ears are yellow with white tips. The skull is large and strongly arched, the interorbital region is very narrow and the **nasals** are relatively long. The general shape of the skull is unlike that of other pikas, but is an extreme culmination of the tendency for the skull to become highly arched as in black-lipped pika *O. curzoniae* and Ladak pika. There are no fenestrae in the frontals.

Distribution

Known only from the Arkatag Range, a spur of the Kunlun Mountains, west of the junction of Xinjiang, Xizang and Qinghai, PRC. They were recently found near Aqqikkol Lake (37°09'N, 88°11'E, 4,260m above sea level; Zheng 1986), not far south of the type locality. The type locality is usually given as Guldsha Valley or "Dolina vetrov" (Valley of the Winds) in the original description, but this is inexact. Buchner (1894) noted that Kozlov's pika was not found in the Guldsha Valley itself (which was occupied by two other species, the black-lipped pika and Ladak pika). Instead, it was found only on the pass above Guldsha Valley and to the west of the pass in the valley of the Dimnalyk River, a tributary of the Cherchen River. The species was also found by members of Prezhevalski's expeditions at two other places: "Kuzuk-Kakty Pass" and the vicinity of the village of Arkatag (36°50'N, 87°20'E). Another possible locality, Ikhe-Tsaidemin Nur (= Lake) (37°50'N, 95°00'E?) needs confirmation. (See Fig. 3.8).

Habitat

Occupies alpine meadow tundra and digs holes in the swelling mounds of saline loess on the Guldsha Pass (Buchner 1894).

Ecology

Unknown.

Behavior

Lives in groups and is diurnally active.

Reproduction

One litter is produced per year (Zheng 1989).

Ladak Pika

Ochotona ladacensis (Günther 1875)

Taxonomy

The original description of this monotypic species was based on specimens originally assigned to the black-lipped pika *O. curzoniae*. All modern authors consider it to be a distinct species (Argyropulo 1948, Ellerman and Morrison-Scott 1951, Gureev 1964, Corbet 1978, Honacki, Kinman and Koeppl 1982, Weston 1982, Feng and Zheng 1985, Feng, Cai and Zheng 1986). It most closely resembles Pallas's pika *O.*

pallasi, being a large pale pika with a very narrow interorbital region; however, the two species are completely allopatric in distribution. The Ladak pika differs from Pallas's pika in having a relatively small tympanic **bullae** and more highly arched cranium. It often has the incisive and anterior palatal foramina completely separate, but with a strong constriction demarking them, as does Kozlov's pika *O. koslowi*. A similar condition is also seen in the Turkestan red pika, *O. rutila*, red-eared pika *O. erythrotis* and Glover's pika *O. gloveri*.

The Ladak pika is broadly sympatric on the Qinghai-Xizang (Tibetan) Plateau with the black-lipped pika *O. curzoniae*. They may be distinguished by the much smaller size of the latter and the wide confluence between incisive and anterior palatal foramina.

Status and Summary

Poorly known.

Description

Pelage in summer is light brownish-gray dorsally with yellowish white underparts. Exterior sides of the ear are distinctively rust-colored. As noted above, the skull is large and arched, the confluent incisive and palatine foramina are narrowly constricted anteriorly and the tympanic bullae are relatively small.

Distribution

Found at high elevations in the mountains of Kashmir, India; Qinghai, Xizang and Xinjiang, China. (See Fig. 3.6).

Habitat

Lives at approximately 4,300-5,450m elevation in extremely barren places (Biichner 1894; Zheng 1989). The only vegetation in some localities occupied by the Ladak pika are widely dispersed clumps of cushion plants *Primula* (Buchner 1894) or *Carex moorcroftii* and *Arenaria musciformis* (Feng, Cai and Zheng 1986, Zheng 1989).

Ecology

The Ladak pika digs huge holes. It is sympatric with the black-lipped pika in the Guldsha Valley (due east from the Guldsha Pass) and at least parapatric with Kozov's pika (Buchner 1894). Based on specimens collected by Pevtsov and currently housed in the Zoological Institute (Leningrad), the Ladak pika and Kozlov's pika may be sympatric near the northern edge of the Arkatag Range.

In the Guldsha Valley Ladak pikas feed only on the roots of *Primula* in winter (Buchner 1894). Erbajeva (1988) claims that the long incisors of this species are adapted for this type of feeding.

Behavior

Upon being startled by man or a predator, these pikas retreat into their burrow while emitting a high abrupt squeak (Buchner 1894).

Reproduction

The reproductive season is in late June and early July (Zheng 1989).

Large-eared Pika *Ochotona macrotis* (Günther 1875)

Subspecies: *Ochotona macrotis baltina* Thomas 1922; *Ochotona macrotis chinensis* Thomas 1911b; *Ochotona macrotis macrotis* (Günther 1875); *Ochotona macrotis sacana* Thomas 1914; *Ochotona macrotis wollastoni* Thomas and Hinton 1922

Taxonomy

The large-eared pika *O. macrotis* has been considered conspecific with Royle's pika *O. roylei* by Argyropulo (1948), Gureev (1964) and Corbet (1978). Here it is considered distinct based on the analyses of Thomas and Hinton (1922), Ellerman and Morrison-Scott (1951), Honacki, Kinman and Koeppl (1982), Weston (1982), Feng and Zheng (1985) and Feng, Cai and Zheng (1986) and our own study, as well as the ecological investigations of Abe (1971), Kawamichi (1971a) and Mitchell (1978, 1981) who observed the two species in their area of sympatry. Examination of the holotypes of *baltina*, *chinensis*, *sacana* and *wollastoni* from the BMNH makes it evident that all of these named subspecies are conspecific. All share the characteristics of *macrotis*; in comparison with Royle's pika *O. roylei* they average larger in size, with paler coloration, larger, broader ears with long, dense hairs inside, frontal foramina usually well-developed and symmetrical, somewhat larger bullae and wider, more highly arched skulls. The diploid chromosome number = 62 (Vorontsov and Ivanitskaya 1973).

Status and Summary

There are currently no known threats to the distribution or abundance of this species throughout its range.

Description

Of moderate size, but averages larger than most Royle's pikas. The general color above is pale brownish gray with an ochre tinge. Along the sides of the face, across the shoulders and from the nose over the occiput, the general grayish color is tinged with rufous, which is more marked during summer. In winter the dorsal color changes to a dense fluffy pale gray with a tinge of straw-yellow. The belly ranges from white to dirty-white in summer and winter. There are usually two small (3 by 1.5mm) oval foramina above and in front of the orbit at the anterior end of the frontal bones.

As can be surmised by the apparent close taxonomic relationship between the large-eared and Royle's pikas, the appearance of these two species is superficially similar. The large-eared can be distinguished from Royle's pika using the following characteristics:

- the inside of the ears is thickly clad with longer hairs in the large-eared pika;

- the head and front are washed with a pale russet color instead of the brilliant rufous brown in Royle's pika; and
- on average the ears are broader in the large-eared pika (Feng and Zheng 1985).

Distribution

Found in the Pamir Mountains and western Tien Shan (Tadzhik SSR, Kirgiz SSR and southeast Kazakh SSR, Soviet Union); the Hindu Kush (northeastern Afghanistan); Karakoram Range (Pakistan); Himalayan Mountains (northern India; northern Nepal; Bhutan; adjacent Xizang, China); and the Kunlun and associated ranges across central western China (Xizang, Xinjiang, Qinghai) and westward into the high mountains of Sichuan and Yunnan Provinces, China. (See Fig. 3.1).

Habitat

A high altitude rock-dwelling pika (Ognev 1940, Abdusalyamov 1962, Bernstein 1970, Kawamichi 1971a, Mitchell 1978, 1981, Sludski *et al.* 1980, Feng, Cai and Zheng 1986, Zheng 1989). It inhabits stationary rock scree in open alpine areas as well as within spruce forests. The alpine desert in the Pamir, Tien Shan, Kunlun and other ranges inhabited by large-eared pikas is apparently lacking in snow cover most of the year (Ognev 1940). Its altitudinal range may extend from 2,500-4,000m to as high as 6,130m (Thomas and Hinton 1922). When found in the same mountain range, the distribution of large-eared pikas is higher than that of Royle's pikas (Kawamichi 1971a).

Ecology

Populations remain relatively constant in size over time, although densities at different locations may range from six to eighteen animals per ha (Bernstein 1970). However, at Chong-Kyzyl-Su Valley, the place that Bernstein conducted her investigations, no pikas could be located in 1977 (N.A. Formozov, unpublished data). Bernstein and Klevezal (1965) determined that yearlings comprised 58% of their study population and that some individuals lived to be three years old.

At least some populations of the large-eared pika do not cache food in haypiles for the winter, as do most other species of pikas (Ognev 1940, Bernstein 1970, Kawamichi 1971a). The lack of snow found in their habitat apparently allows for year-round foraging.

Behavior

The large-eared pika apparently lives in family group territories controlled by a pair of breeding adults (Abdusalyamov 1962, Kawamichi 1971a). Bernstein (1970) supposes that this species does not form a stable couple as does the Turkestan red pika *O. rutila*. She came to this conclusion because she caught four males in close proximity to a single female. However, many males may visit a single female in the northern pika *O. hyperborea*, a species that does form couples. Bernstein (1970) did comment that it was difficult to keep track of the animals she was observing because they were not

individually marked. In his behavioral study Kawamichi (1971a) witnessed no overlap between adult females. Although infrequent, all territorial invasions were by males.

The development of calling behavior in this species is weak compared to most other pikas (Ognev 1940, Kawamichi 1971a). In the event of alarm, the large-eared pika quickly escapes while uttering three to four syllable calls similar to those of the Turkestan red pika. In the fall, in dense populations, these pikas utter occasional sharp whistles. Sometimes conspecifics answer this call with one of the same structure (Bernstein 1970).

Kawamichi (1971a) stated that the lack of vocalizations in the large-eared pika is related to not having a **haypile** to defend. This comment does not correspond with data from other species. The Turkestan red pika stores large quantities of hay, but is more silent than the large-eared pika. The Afghan pika *O. rufescens* is one of the most silent of the pikas and stores hay twice a year (see those accounts).

Reproduction

Litter sizes are small, like those of other talus-dwelling pikas, with two to three young (Abdusalyamov 1962); $\bar{x} = 5$, range 3-7 (Zimina 1962); and 1-4 (Mitchell 1978, 1981). Usually two litters are conceived per year (Abdusalyamov 1962, Zimina 1962, Mitchell 1978, 1981) and, in most populations, individuals **first** breed as yearlings (Zimina 1962). Bernstein (1970) has conducted the most thorough investigation of reproduction in the large-eared pika and found that litter size varied throughout the range, being higher in populations with increased mortality and less constant population size. Also associated with these variables is an increase in dispersal. Females in one population (*O. m. sacana* from talus near a spruce forest in the Terskey-Alatau Range) had three litters per year with two to six young ($\bar{x} = 4.0$). Mean litter size increased from the first ($\bar{x} = 2.8$) to the last ($\bar{x} = 5.0$). Yearlings did not breed. Adult females in another population (*O. wt. macrotis* from the Tien Shan uplands) had no fewer than three litters per year, and some probably four. Average litter size was 5.8 (range 4-8). Litter size decreased from June ($\bar{x} = 6.2$) to August ($\bar{x} = 4.9$). All young females from the first litters also bred and some of them had two litters with three to five young ($\bar{x} = 4.5$).

Muli Pika

Ochotona muliensis Pen et al. 1962

Taxonomy

This form, when it was originally described, was assigned to Glover's pika *O. gloveri*, but now it is considered to be distinct (Feng and Zheng 1985). However, more study is needed to confirm its independent status. As in the case of the **Himalayan** pika *O. himalayana*, the Muli pika is differentiated from Glover's pika largely on the basis of its lack of foraminae on the frontals. This variable character may not be sufficient to ensure its independent status.

Status and Summary

This species is rare, only several specimens exist and it has not been recorded for over 25 years. It may be that chemical control directed at other vertebrate species has threatened its existence.

Description

The head is very faintly tinged with rusty-buff hair and the back of the ears is chestnut or yellow-orange in color. The Muli pika differs from Glover's pika in that it lacks the small oval **foramen** at the anterior dorsal surface of each frontal bone, has relatively shorter nasals and a broader rostrum (Feng and Zheng 1985).

Distribution

Western Sichuan, China. (See Fig. 3.5).

Habitat

Inhabits thicket and steppe habitat. In this respect it appears to differ from Glover's pika, which occupies talus and other rocky habitats.

Ecology, Behavior and Reproduction

Unknown.

Nubra Pika

Ochotona nubrica Thomas 1922

Subspecies: *Ochotona nubrica lhasaensis* Feng and Kao 1974 (includes *lama*); *Ochotona nubrica nubrica* Thomas 1922 (includes *aliensis*).

Taxonomy

Although in his original description Thomas (1922) referred to *nubrica* as a "small species in the *roylei* group," he then went on to point out a number of significant ways in which it differed from Royle's pika *O. roylei*. Corbet (1978) tentatively assigned *lama* (Mitchell and Punzo 1975) to Royle's pika *O. roylei* and *nubrica* to the Moupin pika *O. thibetana*, whereas Ellerman and Morrison-Scott (1951) placed *nubrica* in the steppe pika *O. pusilla*. *O. lama* Mitchell and Punzo 1975 and *O. thibetana aliensis* Zheng 1979 were then combined as *O. thibetana lama* by Feng, Cai and Zheng (1986). Mitchell (1978) had compared *lama* with five other species from Nepal, but not to *thibetana* or *nubrica*.

In addition to the original type series of *nubrica* (four specimens), there are four additional specimens in the BMNH, one in the FMNH and two in the NMNH, all from Kashmir; four additional specimens from the Kashmir border region are in the AMNH. The holotype and two additional specimens of *lama* are in the Royal Ontario Museum, Toronto (ROM). One specimen identifiable as *O. nubrica ihasaensis* (= *lama*), from Nepal, is also in the FMNH. Finally, three specimens of *Zhasaensis* from the type locality have been examined. All of these specimens agree in size,

Pallas's Pika
***Ochotona pallasi* (Gray 1867)**

pelage color and skull characters, being much paler than the Moupin pika *O. thibetana* and more nearly resembling the black-lipped pika *O. curzoniae* in winter pelage. Degree of saturation of pelage color appears (in the few specimens available) to vary clinally from west to east. Specimens from Kashmir (*O. n. nubrica*) are palest, while those from northern Nepal and the vicinity of Lhasa (*O. n. Zhasaensis*) have a somewhat darker, richer sandy dorsal pelage, with more black guard hairs intermixed. The nearest populations of the Moupin pika *O. thibetana* are *O. t. sikimaria* on the more temperate moist southern slope of the Himalayas and *O. t. nangqenica* from the forested headwaters of the great rivers (Mekong, etc.) that originate on the southeast corner of the Tibetan Plateau. The nubra pika *O. nubrica* differs from the Moupin pika *thibetana* (as Feng and Kao 1974 recognized in their description of *lhasaensis*) "in being sandy brownish above and paler gray below, with a distinct buffy color extending down along the midline of the belly," whereas subspecies of *thibetana* are "dull brown or rufous brown" dorsally. The feet of *nubrica* are brownish gray instead of dull brown (Feng and Kao 1974). In addition, *nubrica* has a distinct light patch on the outer surface of the ear that is lacking in *thibetana* and external and cranial measurements average larger than adjacent populations of *thibetana*.

Given the scarcity of available specimens, it is possible that further collecting will demonstrate an intergradation between *O. n. lhasaensis* and *O. t. nangqenica*. However, based on existing data, we recognize them as distinct species.

Status and Summary

Unknown.

Description

The skull is fairly flat, larger than the Moupin pika but smaller than Royle's pika, relatively narrow, but with a fairly broad interorbital and short rostrum. Palatal foramina are widely expanded posteriorly, whereas the bullae are relatively small and narrow.

Distribution

From the limited data available, the nubra pika seems to be a trans-Himalayan species with a narrow range stretching along the Qinghai-Xizang (Tibetan) Plateau from Ladak on the west to eastern Xizang on the east. (See Fig. 3.5).

Habitat

According to the collectors of the type series, the nubra pika inhabits "thick jungle or scrub," by which they presumably mean subalpine or alpine shrubs, implying that this is a burrowing, rather than a talus-dwelling species. The large-eared pika *O. macrotis*, a talus inhabitant, was also reported to occur in the same area. In Nepal, the subspecies *O. nubrica Zhasaensis* lives in alpine steppe habitat and also seems to be a burrowing form (Mitchell 1978).

Ecology, Behavior and Reproduction

Unknown.

Subspecies: *Ochotona pallasi hamica* Thomas 1912b; *Ochotona pallasi pallasi* (Gray 1867) (includes *opaca*); *Ochotona pallasi pricei* Thomas 1911a; *Ochotona pallasi sunidica* Ma, Lin and Li 1980

Taxonomy

This is a generally accepted **taxon**, called *O. pricei* in much of the older literature (Ognev 1940, Vinogradov and Argyropulo 1941, Argyropulo 1948, Gureev 1964). Recent treatments now use the senior **name**, *pallasi*, *pricei* being the junior synonym of the species epithet, but a valid subspecies name (Corbet 1978, Honacki, Kinman and Koepl 1980, Sludski *et al.* 1980, Sokolov and Orlov 1980, Weston 1982, Feng and Zheng 1985).

Three subspecies are currently widely recognized: *O. p. pallasi* in northeastern Kazakhstan, Soviet Union; *O. p. pricei* in Mongolia, southwestern Tuva ASSR, Soviet Union and Xinjiang, China, along the Mongolian border; and *O. p. hamica* in the Karlik Shan north of Hami, Xinjiang, China and perhaps southern Mongolia. The subspecies *sunidica* has only recently been described and is poorly known. The form *sushkini*, formerly placed in Pallas's pika *O. pallasi*, is here referred to the alpine pika *O. alpina* (see that account). The **trenchant biological differences** in ecology and behavior between the forms *pallasi* and *pricei* (see below) suggest the possibility that they may be specifically distinct.

Status and Summary

O. p. hamica is poorly known and only the type series (six specimens) is known to exist. There have been no records from its Karlik Shan locality (Xinjiang, China) for over half a century. The range of the subspecies *hamica* in the Tsagaan Bogd Uul (Mountains) (Mongolian People's Republic) is enigmatic. Its population there has steadily declined over the past 4,500 years (Kniazhev, Savinetski and Sokolovskaya 1986, Kniazhev and Savinetski 1988). The percentage of Pallas's pika bones to that of all small mammals was 23.6% between 3,000 and 4,500 years ago, 7.8% between 2,000 and 3,000 years ago, 7.3% between 1,500 and 2,000 years ago, and only 0.4% for the period encompassing the past 200 years. Kniazhev, Savinetski and Sokolovskaya (1986) and Kniazhev and Savinetski (1988) feel that global drying of climate in the southern Gobi over the past 200 years may be responsible for this downward trend in the representation of pikas in the fauna. *O. p. hamica* has not been collected in the Tsagaan Bogd Uul in historical time, although in 1979 K.A. Rogovin (personal communication) heard pikas and located fresh scats there. *O. p. hamica* also may be found currently in the Atas Bogd Uul (MPR). Bannikov (1951) apparently caught one animal there in 1943 and his personal diary (Anna Bannikova, personal communication) states that there was a reasonable population at the top of the mountains. In summer 1988 Kh. Suhbat (personal communication) visited this place, but did not find any pikas. Scientists who work at the Great Gobi Biosphere Reserve have never recorded pikas in either the Atas Bogd Uul or in

the Tsagaan Bogd Uul throughout their work. In summary, *hamica* lives in isolated mountains in the Gobi Desert and, due to changes in climate, small population size, isolation and potential habitat degradation, should be considered as seriously endangered.

O. p. sunidica is similarly isolated from the main distribution of the species and may also be at risk. A status survey is needed to evaluate this.

The isolated population of *O. p. pricei* from the Choyr Mountains (southeast of Ulaanbaatar, MPR; 46°40'N; 109°E) is currently very depressed and should be considered threatened. Similarly, other populations of *pricei* have declined over the centuries, especially those near its southern distributional boundary (Denisman *et al.* 1989). On the Dzhinst-Ula Ridge pikas comprised 38% of the bones of the prey of owls eleven centuries ago. This figure declined to 28% ten centuries ago and 21% six centuries ago. Only one migrating juvenile was seen at this site in 1980 (K. A. Rogovin, personal communication) and none live there now (Denisman *et al.* 1989). The range of *O. p. pallasii* also seems to have decreased. This form has disappeared from the Dzhambul Mountains and only isolated populations now exist in the Kyzkash Mountains and in the hills east of the Aktogai railroad station. These isolated populations are very small and vulnerable (Sludski *et al.* 1980).

On the other hand, *O. p. pricei* has been considered a pest species in southwestern Tuva ASSR, USSR, because it is considered a focus for plague (Krylova 1976, Shilova *et al.* 1977). Control of *O. p. pricei* in this region has now ceased (MA. Erbajeva, personal communication). *O. p. pricei* is heavily controlled in China near the border of Mongolia (Fan, personal communication).

O. p. pallasii was also trapped for the fur industry in Kazakh SSR. All pika species and some gerbils *Rhombomys opimus*, *Meriones tamareiscinus* have the same common name in Russian ("pishchukha"), thus it is difficult to examine closely the numbers of *Ochotona* trapped. In some years a few thousand small pishchukhas were trapped in the Karaganda region (where *O. pallasii* and *O. pusilla* are common), but only 300-350 were actually pikas (Sludski *et al.* 1980).

Description

This is a fairly large pika, similar in size to the alpine pika. In summer the dorsal pelage of Pallas's pika is uniformly sandy buff in color; the ventral surface is marked by only the faintest suggestion of a buffy wash. In winter the head and body are pale gray, while the hindquarters are slightly brighter with a buffy tint. The alpine pika is darker in both summer and winter pelage. The toe pads are bare and black in stark contrast to the heavily furred feet of the sympatric Daurian pika *O. daurica*. The skull is moderately large and somewhat arched. The interorbital width is less than in the alpine pika and the tympanic bullae are comparatively large. There are no fenestrae present in the frontals and the incisive and anterior palatine foramina are completely separated. The diploid chromosome number is 38, compared to 40 in northern pika and 42 in alpine pika (Vorontsov and Ivanitskaya 1973).

Distribution

Distributed discontinuously throughout the Gobi Desert region from Kazakh SSR, Tuva ASSR, Soviet Union; Mongolian People's Republic; western Xinjiang, Nei Monggol, China. The range of Pallas's pika is broken by more disjunctions than are seen in other species of burrowing pikas. (See Fig. 3.6).

Habitat

Habitat preference is intermediate between burrowing and talus-dwelling pikas; it may inhabit either open desert or rocky areas. Pallas's pikas typically burrow in steep cliff faces (Formozov 1929, Allen 1938, Ognev 1940, Vinogradov and Argyropulo 1941, Smirnov 1974, 1985, 1986, Zevegmid 1975, Eshchelkin 1978, Sludski *et al.* 1980, Wang and Yang 1983, Ma *et al.* 1987). There are distinct habitat differences between the various subspecies: almost all populations of *O. p. pallasii* live in rocky situations, whereas *O. p. pricei* usually occupies arid steppe environments where it may either burrow or live in rocks (Formozov 1985). *O. p. sunidica* dwells in cracks of rocks (Ma, Lin and Li 1980).

Ecology

Population densities of *O. p. pallasii* may vary greatly and reach levels as high as 100/ha (Smirnov 1974). Zevegmid (1975), commenting on the number of families of *O. p. pricei* found per ha, also concluded that this subspecies may attain high densities. Zevegmid (1975) related an instance in which a population high of ground squirrels *Spermophilus alaschanicus* so overgrazed an area that *O. p. pricei* numbers were significantly reduced. In addition, throughout its range populations of Pallas's pika are frequently isolated from one another, even when separated by suitable habitat. In these instances local populations are subject to frequent extinction; these areas are rarely recolonised due to their poor vagility (Ognev 1940).

Pallas's pikas appear to be relatively long-lived. Krylova (1973) determined that natural mortality in *O. p. pricei* was about 50% per year and that maximum longevity was four years. Two-year-old animals comprised 20% of the summer population. Shubin (1966) stated that young *O. p. pallasii* are more numerous than those in steppe pika *O. pusilla* populations.

Smirnov (1986) determined that when Pallas's pikas lives in close proximity to steppe pikas *O. pusilla* (with *pallasii*) or Daurian pikas (with *pricei*), little overlap, hence competition for resources, occurs because of the difference in habitats selected by these species.

O. p. pallasii make relatively large haypiles (80-100cm high) on the ground over burrow entrances (Smirnov 1974). Typically the caches of *O. p. pallasii* are stored under rocks, however. Wang and Yang (1983) indicate that *O. p. pricei* also constructs a large haypile.

O. p. pricei constructs burrows with many entrances; in one locality the average number of entrances was 28, with a maximum of 80 (Kholodova 1975). Many of these holes are

associated with the abandoned burrows of *Marmota sibirica* (Demin 1962). In southwestern Tuva, certain plants (*Euphorbia altaica* and some crucifers) reach high abundance and flower only above pika burrows. *Artemisia* grows only above the burrows of pikas (Kholodova 1975).

Behavior

There are significant differences in the behavior of *O. p. pallasi* and *O. p. pricei*. The home range of males of *O. p. pallasi* includes the home ranges of up to six females during the summer. The size of the home range of males ($\bar{x} = 5200\text{m}^2$) is six times larger than that of females ($\bar{x} = 800\text{m}^2$) (Proskurina, Formozov and Derviz 1985). The social organization of *O. p. pricei* during the breeding season is similar to that of *O. p. pallasi* (Ryl'nikov, personal communication) and the mating system appears to be primarily polygynous (Formozov 1985). Most individuals remain close to their burrows (Smirnov 1974). Males may demonstrate high levels of intrasexual aggression, even though their burrows can be separated by only three to four metres (Smirnov 1974; Sludski *et al.* 1980; Proskurina, Formozov and Derviz 1985). When individuals trespass onto the territories of neighbors they may be killed by bites inflicted by the occupant. Typical aggressive interactions involve chases and boxing. Boxing occurs for as long as three to fifteen seconds per bout (Okunev and Zonov 1980). In contrast, the duration of bouts of boxing in other forms (*O. p. pallasi*, Daurian pika, steppe pika, northern pika) is often approximately one second (just a short push). Aggressive relationships are ten times more frequent in *O. p. pricei* than in *O. p. pallasi* (Formozov and Proskurina 1980).

Males and females that share home ranges rarely exhibit aggression and juveniles are tolerated in the burrows of adults even if there is another brood (*O. p. pallasi*; Smirnov 1974). Young may be chased out of their natal burrow system when they become sexually mature. This behavior is coincident with the division into separate territories of males and females following the breeding season (*O. p. pricei*). For example, mean area of territories in August is 403m^2 . In January, the territory size varies from 129m^2 (when the snow cover is from 3-4cm deep) to 9m^2 (when the snow is from 15-40cm deep) (Okunev and Zonov 1980). Home ranges of *O. p. pricei* decrease when population density increases (Okunev and Zonov 1980).

A male *O. p. pallasi* regularly cruises throughout its home range. In meetings with females, they utter soft quiet trills. Males and females avoid direct contact. The male and female have separate core areas of their respective home ranges and separate stores of food. The male protects its core area from females, but that of females may be visited by males, and males frequently steal from the stores of females (Formozov and Proskurina 1980).

The vocalizations of *O. p. pallasi* and *O. p. pricei* differ greatly. The most important difference is that *O. p. pallasi* has a song or long call but *O. p. pricei* does not. This long call is a fast trill uttered by both males and females. Alarm calls of these subspecies also vary in their dynamic spectrum of fre-

quency (Formozov and Proskurina 1980).

Both subspecies mark home ranges by rubbing the neck gland on the corners of stones and urinating on piles of their hard pellets. *O. p. pricei* constructs little pyramids from sticky fecal pellets near the lateral entrance to their burrows, their territory borders and places of frequent conflict. *O. p. pallasi* marks its entire home range.

In late summer and fall, *O. p. pricei* collects stones and puts them in piles. The mean weight of the stones is 45g (5-170g). Pikas close more of their burrow entrances with these stones before the onset of winter (Okunev and Zonov 1980).

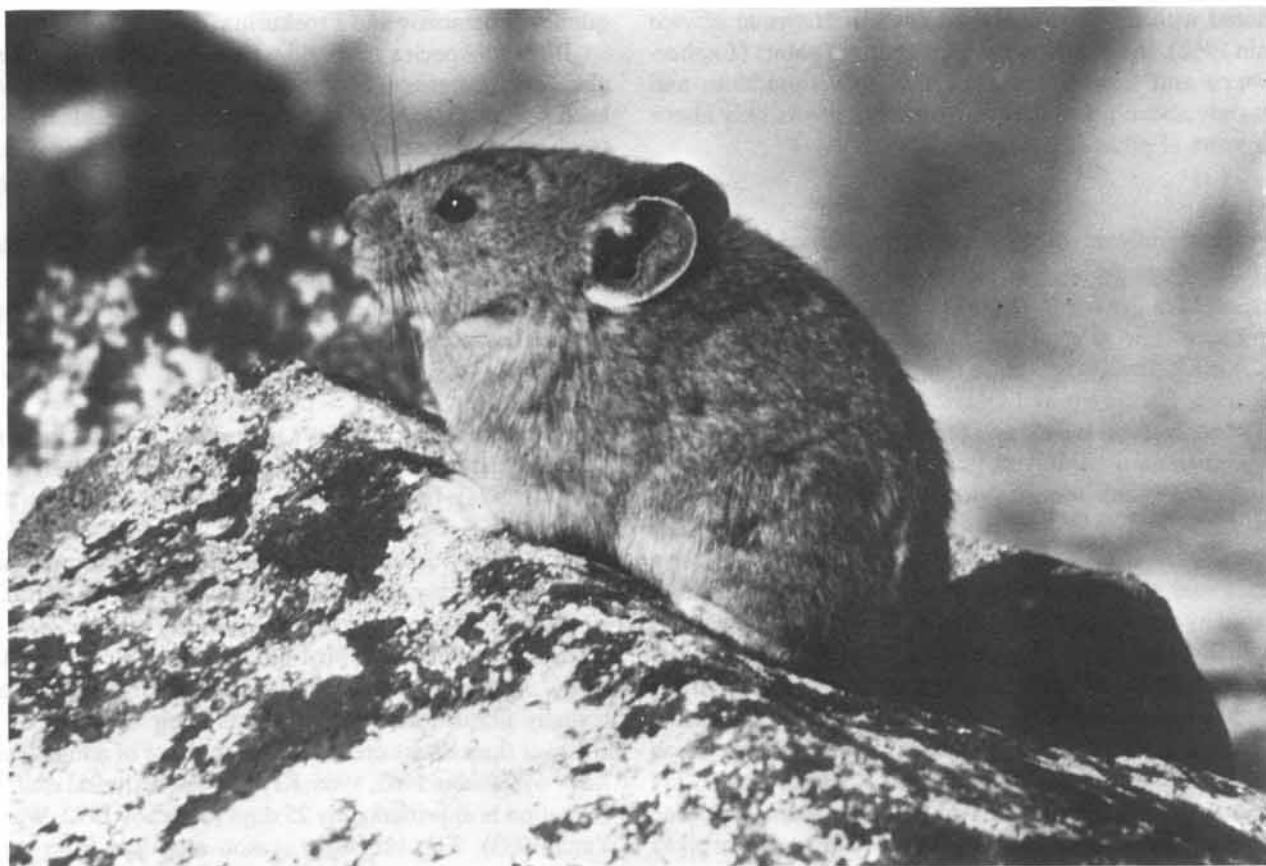
Reproduction

The fecundity rate of Pallas's pikas is high. Adult litter size in *O. p. pricei* ranges from 1-12 (Lazarev 1968), to 1-10 ($\bar{x} = 6.5$; Krylova 1974). In *O. p. pallasi*, litter size ranges from $\bar{x} = 7.5$ (Shubin 1965, 1966) to $\bar{x} = 8$ (range 2-13; Sludski *et al.* 1980). Several litters are produced per year with a post-partum estrus (both subspecies; Ognev 1940, Krylova 1974, Sludski *et al.* 1980). In *O. p. pallasi*, all adult females breed at least twice, but the occurrence of third litters is variable (Sludski *et al.* 1980). At least some juveniles born in first litters become sexually mature and reproduce in their summer of birth, however their litters are smaller than those of adults (range 3-7, $\bar{x} = 5$) (Shubin 1965, 1966; Krylova 1974; Sludski *et al.* 1980). Gestation is approximately 25 days (Smirnov 1972, Wang and Yang 1983). The breeding season may last from April to August (Ma *et al.* 1987). *O. p. pallasi* breed from early April until May or June (Sludski *et al.* 1980).

American Pika

Ochotona princeps (Richardson 1828)

Subspecies: *Ochotona princeps albata* Grinnell 1912a; *Ochotona princeps barnesi* Durrant and Lee 1955; *Ochotona princeps brooksi* Howell 1924; *Ochotona princeps brunnescens* Howell 1919; *Ochotona princeps cinnamomea* Allen 1905; *Ochotonaprinceps clamosa* Hall and Bowlus 1938; *Ochotona princeps cuppes* Bangs 1899; *Ochotona princeps fenisex* Osgood 1913; *Ochotona princeps figginsii* Allen 1912; *Ochotona princeps fumosa* Howell 1919; *Ochotona princeps fuscipes* Howell 1919; *Ochotona princeps goldmani* Howell 1924; *Ochotona princeps howelli* Borell 1931; *Ochotona princeps incana* Howell 1919; *Ochotona princeps jewetti* Howell 1919; *Ochotona princeps lasalensis* Durrant and Lee 1955; *Ochotona princeps lemhi* Howell 1919; *Ochotona princeps littoralis* Cowen 1955; *Ochotona princeps lutenscens* Howell 1919; *Ochotona princeps moorei* Gardner 1950; *Ochotona princeps muiri* Grinnell and Storer 1916; *Ochotona princeps nevadensis* Howell 1919; *Ochotona princeps nigrescens* Bailey 1913; *Ochotona princeps obscura* Long 1965; *Ochotona princeps princeps* (Richardson 1828); *Ochotona princeps saturata* Cowen 1955; *Ochotona princeps saxatilis* Bangs 1899; *Ochotona princeps schisticeps* (Merriam 1889); *Ochotona princeps septentrionalis* Cowen and Racey 1946; *Ochotona princeps*



American pika *Ochotona princeps*, Rocky Mountains, Colorado (Photo by Andrew Smith)

sheltoni Grinnell 1918; *Ochotona princeps taylori* Grinnell 1912b; *Ochotona princeps tutelata* Hall 1934; *Ochotona princeps uinta* Hollister 1912b; *Ochotona princeps utahensis* Hall and Hayward 1941; *Ochotona princeps ventorum* Howell 1919; *Ochotona princeps wasatchensis* Durrant and Lee 1955

Taxonomy

The American pika is closely similar to the alpine pika *O. alpina*, northern pika *O. hyperborea* and collared pika *O. collaris* and has been included with these forms in various treatments. Broadbooks (1965) and Youngman (1975) included *O. collaris* in *princeps*. Argyropulo (1948), Gureev (1964) and Corbet (1978) treated *princeps* under *O. alpina*, along with *O. collaris* and *O. hyperborea*. Weston (1981, 1982) determined that *princeps* and *collaris* are each independent and are distinct from the Asian forms. Corbet and Hill (1986) treated the four species as independent. In addition, the diploid chromosome number of the American pika *O. princeps* is 68 (as is that of the collared pika *O. collaris*; Hsu and Benirschke 1971), while $2N = 40$ in northern pika *O. hyperborea* and 42 in alpine pika *O. alpina* (Vorontsov and Ivanitskaya 1973).

The 36 subspecies of *O. princeps* were reviewed by Hall (1981), but no modern systematic revision of the species has been undertaken. Smith and Weston (1990) review the systematics and biology of the species.

Status and Summary

In spite of the discontinuous range of the 36 subspecies and isolated populations, there appear to be no current threats to the distribution or abundance of most forms of the American pika. However, some isolated populations in the Great Basin of the United States, including one from a subspecies type locality (*O. p. tutelata*), have disappeared in recent years (Hafner and Sullivan, personal communication). Other insular populations that may be at risk are *O. p. goldmani*, *O. p. obscura* and *O. p. nevadensis*. A recent electrophoretic survey indicated that *O. p. nevadensis* may have lost most, or all, of its genetic variability (D.J. Hafner and R.M. Sullivan, personal communication).

Description

The American pika is intermediate in size among the pikas and there is considerable interpopulation variation. In summer dorsal pelage ranges from grayish to cinnamon-brown, often richly colored with tawny or ochraceous. Winter pelage is grayer and nearly twice as long as the summer pelage. The dense underfur is usually slate-gray or lead colored. Ventral pelage is predominantly whitish with a buffy wash. Coastal subspecies tend to be darker than those found further inland (except those forms occurring on dark lava beds). There are six mammae. The skull is slightly rounded in profile and the interorbital region is broad and flat. The rostrum is slender



Habitat of American pika *Ochotona princeps* on mine tailings at Bodie, California (Photo by Andrew Smith)

and the nasals are widest anteriorly.

Distribution

The American pika is distributed discontinuously in mountainous areas throughout western North America (British Columbia, Alberta, Canada; Washington, Oregon, Nevada, California, Idaho, Montana, Wyoming, Utah, Colorado, New Mexico, United States). In the northern part of its range this species is found at elevations ranging from sea level to 3,000m; however to the south the lower elevational limit becomes progressively higher. Near the southern limits of its distributional range it is uncommon to find pikas at elevations lower than 2,500m (Grinnell 1917, Smith 1974a). (See Fig. 3.3).

Habitat

Throughout its range the American pika is habitat specific to talus or piles of broken rock fringed by suitable vegetation. The talus habitat occupied by pikas is often distributed patchily, leading to an island-like population structure (Smith 1974a, 1974b, 1980).

Ecology

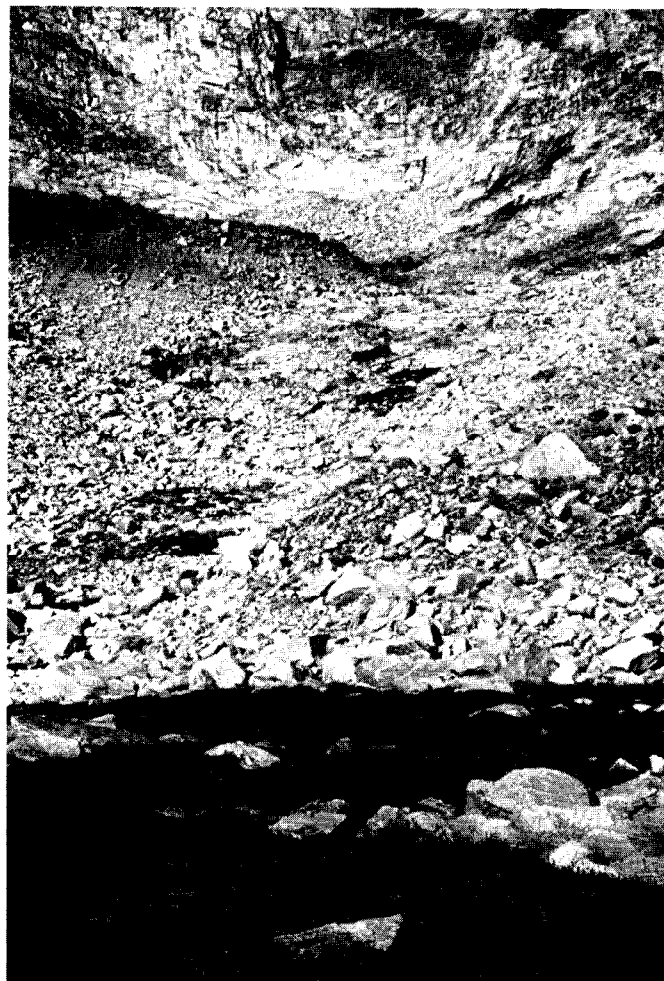
Adults are individually territorial and the sex-ratio of adults is near unity in all studies of fully marked populations (Smith 1981b). Average territory sizes of males and females are similar. Territory size varies seasonally, being significantly larger in early than in late summer (Smith and Ivins 1984). Size of territories averages about 55% of home range size (Smith and Ivins 1986/1987). In most studies density approximates six to ten animals per ha. Spacing of males and females on talus is non-random. Adjacent home ranges tend to be occupied by individuals of the opposite sex and these home ranges are usually occupied sequentially by an animal of the same sex as the previous occupant. Overlap of home ranges is greater and nearest-neighbor distances are less between paired adults than between nearest-neighbors of the opposite sex (Smith and Ivins 1984). Population size is remarkably stable from year to year (A.T. Smith 1978, Southwick et al. 1986). Survivorship is relatively high for a small mammal.

Individuals may live to an age of seven years and average annual mortality rate is 37.46% (Millar and Zwickel 1972a, A.T. Smith 1978).

Extinction of small populations of pikas on isolated patches of habitat is inversely related to patch size. Colonization of vacant patches is not impeded by the vagility of pikas at high elevations where daytime temperatures are low during the time of dispersal. However, at sites near the lower elevational limits of the geographic range of pikas vagility may be influenced by warm temperatures, resulting in relatively restricted colonization success. Ultimately, as probability of colonization decreases at low elevations, colonization is unable to offset extinction and the distributional limit of the range of the American pika is stabilized (Smith 1974a, 1974b, 1980).

The American pika is a generalized herbivore and many studies throughout the geographic range of the species indicate the following patterns:

- differences in species composition of plants harvested are frequent and reflect local variation in the composition of plant communities;



Habitat of the American pika, Sierra Nevada, California (Photo by Andrew Smith)

- at any one locality some plants are preferred over others and some are not harvested at all;
- preferred plants are commonly harvested in a definite sequence that normally corresponds to their seasonal **phenology** (Broadbooks 1965, Millar and Zwickel 1972b, Smith 1974a, Conner 1983a, Huntly, Smith and Ivins 1986, Huntly 1987).

Preferred plants have a significantly higher caloric, protein, lipid and water content than non-preferred plants. Some plants may be ignored due to presence of toxic chemicals (Millar and Zwickel 1972b, Smith 1974a, West 1981). American pikas store caches of food during summer in **haypiles** that can serve as a source of food overwinter. The amount of vegetation stored in **haypiles** may vary with sex (males store more than females), age (adults more than juveniles), the amount of forage available on nearby meadows (more luxuriant meadows yield larger haypiles) and with the distance vegetation has to be transported (the greater the distance, the smaller the haypile). Most **haypiles** are constructed near the talus-meadow interface and these sites appear to be traditional (Millar and Zwickel 1972b, Smith 1974a).

Behavior

The primary mechanism with which American pikas defend their territories is aggression (chases and fights between conspecifics) (Kawamichi 1976, Svendsen 1979, Smith 1981b, Smith and Ivins 1984). Aggressive acts occur rarely (generally less than one act for every ten hours) and normally occur between animals of the same sex. The highest frequency of aggressive acts occurs when unfamiliar animals, for example a resident and an immigrant, come into contact. Individuals frequently intrude on the territories of neighbors, but they usually do so when the resident is inactive (Smith and Ivins 1986). Social cohesion among nearest-neighbor pikas of the opposite sex is maintained by exhibiting social tolerance and engaging in vocal duets of short calls. The paired spatial configuration, its persistence in time and the interplay of aggression and social tolerance leads to the classification of the mating system of the American pika as being facultatively monogamous (Smith and Ivins 1984).

Juveniles are born into the relatively permanent and static social organization of territory holders. The probability of a juvenile living to adult age is directly contingent on its finding a vacant territory to occupy; the appearance of a vacancy is infrequent and unpredictable in time and space. Juveniles face high rates of aggression by unfamiliar adults should they disperse. Also, the likelihood of successful dispersal across non-talus habitat is low. As a result, most young are **philopatric**. There is no sex bias to dispersal (Smith 1987, Smith and Ivins 1983b). One apparent result of this philopatric settlement pattern is a highly inbred population structure and very low levels of genetic heterozygosity within populations (Glover et al. 1977, Tolliver et al. 1985).

The American pika has two frequently used and characteristic vocalizations: the short call and the long call or song

(Smith and Ivins 1984, Conner 1985a). The short call varies geographically, but is uniform within populations (although individuals may be recognized on the basis of their distinctive calls) (Somers 1973, Conner 1982, 1983b, 1985b). Short calls are given in two contexts: as an alarm call to potential predators and to discourage conspecifics from intruding on one's territory. Alarm calls are generally repetitive short calls. Short calls are given by both sexes and all ages, whereas long calls are uttered by adult males primarily during the breeding season (Conner 1983b, 1984, 1985a, Ivins and Smith 1983).

They also communicate by depositing scent marks onto rocks from the enlarged apocrine gland complex found on their cheeks. Pikas are able to discriminate among individuals by the odors emitted from these scent marks. There appears to be a dual function to this behavior:

- territory maintenance and/or advertisement;
- sexual advertisement leading to mating (Svendsen 1979, Meaney 1983, 1987).

Reproduction

Each resident adult female is reproductively equivalent to all others. In the American pika females first reproduce as yearlings and all females initiate two litters per year. Generally only the first litter is successfully weaned, although if it fails the second breeding attempt may be successful. Litter size does not vary with age, habitat productivity, or between first and second litters. There is only slight variability in litter size within a locality. Average litter size among sites also varies little ($\bar{x} = 2.3-3.7$) and may be explained on the basis of spatial and temporal age-specific mortality. Both gestation and time to weaning are approximately 30 days. Males are considered reproductively active when their testes length is greater than 10mm (Millar 1972, 1973, 1974; Smith 1978, Smith and Ivins 1983a).

Steppe or Little Pika *Ochotona pusilla* (Pallas 1768)

Subspecies: *Ochotona pusilla angustifrons* Argyropulo 1932; *Ochotona pusilla pusilla* (Pallas 1768)

Taxonomy

This species has generated relatively little systematic confusion (Argyropulo 1948, Gureev 1964, Corbet 1978, Honacki, Kinman and Koeppl 1982, Weston 1982). Ellerman and Morrison-Scott (1951) included the forms *nubrica*, *forresti* and *osgoodi* in *O. pusilla*. Here *nubrica* and *forresti* are treated as independent species and *osgoodi* as a subspecies of *O. thibetana* (see those accounts).

Status and Summary

The range of the steppe pika has contracted significantly in historical times and it is likely that this pattern has resulted from modification of its preferred steppe-shrub habitat.

Ognev (1940) mentioned that “various data indicate that this species becomes constantly rarer in the Trans-Volga and in western Siberia.” Recently some European populations of *O. pusilla pusilla* were listed as “rare” in the Red Book of the Bashkir Autonomous Republic, Soviet Union (Kuchеров 1987).

Steppe pikas have been trapped for the fur trade, largely to make high quality felt. This activity apparently had no noticeable influence on their populations and has now ceased (Sludski et al. 1980).

Description

This is a small pika. In summer the dorsal pelage is a dark grayish brown with a touch of straw speckling on the back and flanks. The ventral coloration is a dull whitish gray. The winter coat is slightly paler in color compared to summer pelage. The small skull has a relatively flat profile. There are no fenestrae in the frontals and the tympanic bullae are proportionally large. The diploid chromosome number = 68 (Vorontsov and Ivanitskaya 1973).

Distribution

Steppe regions from the upper Volga River and southern Ural Mountains south and east to the border of China, RSFSR and Kazakh SSR, Soviet Union. Although the steppe pika has not been recorded in Xinjiang, China, by any Chinese zoologists (Wang and Yang 1983, Ma et al. 1987), Sludski et al. (1980) suggested that the species dwells on the south slope of the Tarbagatai mountains in China. In the Quaternary and Holocene Periods this species lived in the Crimea, the Ukraine and western Europe (Ognev 1940, Argyropulo 1948). (See Fig. 3.7).

Habitat

This is a characteristic burrowing steppe-dwelling pika (Ognev 1940, Vinogradov and Argyropulo 1941, Dubrovsky 1963, Gureev 1964, Pakizh 1969, Smirnov 1974, Sludski et al. 1980). The steppe pika is found primarily in moist soil which is verdant with thick grass and bushes; where it occurs in arid or desert steppes it is generally found in wet situations (Ognev 1940, Dubrovsky 1963, Smirnov 1974).

Ecology

In general the steppe pika appears to live socially in burrows and to tolerate high densities if conditions permit (Smirnov 1974). Smirnov (1974) determined that the minimum distance between burrows was as little as two to four metres. Various authors note that there are major spatial and temporal changes in population density of the steppe pika. Shubin (1966) determined that the density of pikas in one area ranged from 11/ha in April to 62/ha in June of one year, but crashed to 0.1/ha in April and 0.9/ha in June of the following year. Density may vary with habitat quality, with high densities of up to 80/ha (Dubrovsky 1963; Pakizh 1969).

Smirnov (1986) determined that the steppe pika did not overlap or compete with Pallas's pika *O. pallasi* in areas in which they both occurred, due to differences in their preferred

habitats.

Steppe pikas construct haypiles (Ognev 1940).

Behavior

This is an unusual pika in that it is frequently nocturnal. Its vocalizations are usually heard at late dusk and through the night.

The social organization of the steppe pika has been very poorly studied. Its nocturnal activity and reliance on shrubby habitat make direct observation, such as is possible with diurnal pikas in more open habitats, difficult. Apparently these pikas live in family groups composed of an adult pair and their young (Smirnov 1974, Dubrovsky 1963), although Vinogradov and Argyropulo (1941) and Shubin (1965) state that they live singly. Shubin (1965) relates that in spring the males live as nomads, very often singing from groups of bushes where holes or other signs of the presence of pikas can not be detected. In his study, females living separately as far as 800m from the next nearest pika became pregnant. Shubin (1965) supposes that the mating system is promiscuous (see also Sludski et al. 1980).

This is a very vocal pika (Ognev 1940, Vinogradov and Argyropulo 1941, Dubrovsky 1963). The long call or song is uttered by both males and females. The male's song is a series of long trills of rich low sounds. It can be heard from a distance of two kilometers (Sludski et al. 1980). In captivity females utter songs in the absence of males. Females will often sing in response to the song of a conspecific female. In these cases the female that initiated singing will often chase the responding female (Smirnov and Formozov, unpublished data). The song of females acts to attract males in the field (Smirnov, Snarski and Chetverikova 1987).

Reproduction

Litter size ranges from one to thirteen (6-12, $\bar{x}$ = 8.7, Ognev 1940; 3-13, $\bar{x}$ = 8.5, Shubin 1965; 3-13, $\bar{x}$ = 8.9, Sludski et al. 1980; 1-11, $\bar{x}$ = 5.8, Smirnov 1982). Shubin (1965) indicates that litter size also varies with age (young of the year have smaller litters than adults) and season of reproduction. Adults produce three to five litters per season, whereas young of the year have one to three (Shubin 1965, Smirnov 1982). Maturation of juvenile females takes four to five weeks, while males mature as yearlings (Shubin 1965).

Royle's Pika

Ochotona roylei (Ogilby 1839)

Subspecies: *Ochotona roylei nepalensis* Hodgson 1841; *Ochotona roylei roylei* (Ogilby 1839) (includes *angdawai*, *mittchelli*); *Ochotona roylei wardi* Bonhote 1904

Taxonomy

Several authors include the large-eared pika *O. macrotis* in Royle's pika *O. roylei* (Argyropulo 1948, Gureev 1964, Corbet 1978). Here these forms are considered separate based on the analyses of Thomas and Hinton (1922), Ellerman and Morris-

son-Scott (1951), Honacki, **Kinman** and Koeppel (1982), **Weston** (1982), Feng and Zheng (1985), Feng, Cai and Zheng (1986), our own studies, as well as the ecological investigations of Abe (1971), Kawamichi (1971a) and Mitchell (1978, 1981) who observed the two species in their area of sympatry.

In addition, there has been considerable confusion as to which subspecific forms to include in *O. roylei*. The form *nubrica* was included in *O. thibetana* by Corbet (1978). We consider *nubrica* a distinct species on the basis of extensive comparisons of museum specimens and on zoogeographic grounds (see that account). Corbet (1978) placed the form *forresti* in *O. roylei*, but here it is assigned to its own species based on the analyses of Feng and Zheng (1985), Feng, Cai and Zheng (1986) and our own study. The form *O. lama* Mitchell and Punzo 1975 was also assigned to *O. roylei* by Corbet (1978), but we have accorded this form subspecific status (as a synonym of *Zhasaensis*) under *O. nubrica*.

The species described as *O. angdawai* (Biswas and Khajuria 1955) and *O. mitchelli* (Agrawal and Chakraborty 1971) were synonymised with Royle's pika *O. roylei* by Corbet (1978). In addition, Mitchell (1981) stated that *angdawai* and *mitchelli* "are little more than color phases of *O. roylei*;" *mitchelli* differs slightly in coloration from typical *roylei* in that its fur is more slaty. Here we include both names as synonyms of *O. roylei*. Another recently described species, the Himalayan pika *O. himalayana* (Feng 1973), was also synonymised with *O. roylei* by Corbet (1978), Honacki, **Kinman** and Koeppel (1978) and Weston (1982). However here it is treated separately following its original description (Feng and Zheng 1985 and Feng, Cai and Zheng 1986; see that account). The named forms *baltina* and *chinensis* have sometimes been assigned to *roylei*, but on the basis of study of both holotypes, we conclude that they belong within the large-eared pika *O. macrotis* (see account of *macrotis*). On the other hand, *nepalensis* and *wardi* are clearly races of Royle's pika *O. roylei*. Gureev (1964) gave *nepalensis* full species status and listed *angdawai* as a synonym.

Status and Summary

There are currently no threats to the distribution or abundance of Royle's pika throughout its range.

Description

During summer the head, shoulders and fore part of the body are bright chestnut colored, becoming more vinaceous on the throat. The remainder of the dorsal surface is dark grayish rufous. Ventrally, the coloration ranges from white to grayish-white to dark gray. The winter coat is similar, but may show only traces of, or lack, rufous coloration. In the field the pelage of Royle's pika is very similar to that of the Afghan pika *O. rufescens* (A. Simonetta, personal communication). There may be considerable variability among the various forms. *O. r. wardi* is generally dark. Ears are moderate in size and are sparsely haired. The skull is of moderate size and only slightly arched, less so than in the large-eared pika. The rostrum is short and bullae are relatively small. Frontal fenestrae are present in juveniles, but this condition tends to disappear in

adults, in contrast to the large-eared pika. Royle's pikas have two pairs of mammae (Mitchell 1978).

Distinguishing characteristics between Royle's pikas and large-eared pikas are given in the account on the latter.

Distribution

Along the Himalayan **massif** from Pakistan, through Kashmir, northwestern India, Nepal and adjacent Xizang, China. Its occurrence in the mountains of western China is problematic; records from there probably refer to *O. macrotis chinensis*. (See Fig. 3.7).

Habitat

Royle's pikas are characteristically associated with broken slopes or talus (Kawamichi 1968, 1971a, Abe 1971, Roberts 1977, Mitchell 1978, 1981, Feng, Cai and Zheng 1986). This species generally lives at lower elevations than the large-eared pika, thus occurring in more mesic situations such as rhododendron, deodar or spruce forests. Royle's pika may inhabit the rock wall huts of local people throughout its range (Kawamichi 1968, Abe 1971, Mitchell 1978).

Ecology

Densities reached in Royle's pika populations are low and characteristic of other talus-dwelling pikas. They may attain densities of 12.5/ha (recalculated from Kawamichi 1968).

The caching of food is weakly developed in this species, although they apparently are more likely to construct haypiles than the large-eared pika (Kawamichi 1971a, Roberts 1977, Mitchell 1978, 1981).

Behavior

Royle's pikas appears to live in family groups composed of an adult male and female and their offspring (Kawamichi 1971a, Mitchell 1981).

During winter, in their area of sympatry, this species tends to be crepuscular whereas the large-eared pika is diurnally active (Kawamichi 1971a). In addition, Kawamichi (1971a) noted that during winter Royle's pika was infrequently surface-active even during hours of dawn and dusk.

Royle's pikas vocalize frequently, but these calls may be so faint that they are almost impossible to hear more than a few meters from the caller (Abe 1971, Kawamichi 1971a). On the other hand, Roberts (1977) and Mitchell (1978) describe the call of this species as being a high-pitched piercing whistle, which is louder than the vocalizations of the Afghan pika. A variety of call types may be uttered by Royle's pikas, but their function has not been analyzed (Abe 1971, Kawamichi 1971a).

Reproduction

The fecundity rate is low. Litter size averages three (range 1-5) (Abe 1971, Mitchell 1978, 1981). The breeding season may extend from late spring until late summer and one or two litters may be produced during this time (Roberts 1977, Mitchell 1978, 1981). Apparently animals first become reproductively active as yearlings.

Afghan Pika
***Ochotona mfescens* (Gray 1842)**

Subspecies: *Ochotona rufescens regina* Thomas 1911a; *Ochotona mfescens mfescens* (Gray 1842) (includes *seiana*); *Ochotona rufescens shukurovi* Heptner 1961; *Ochotona rufescens vizier* Thomas 1911a; *Ochotona rufescens vultuma* Thomas 1920

Taxonomy

The only controversies concerning the Afghan pika *O. rufescens* are whether or not the form *vultuma* (from Baluchistan) is a valid subspecies, and whether the form *seiana* (Thomas 1922) should be assigned to this species (see account of the black-lipped pika *O. cunoniae*). The incisive and palatal foramina in the holotype of *vultuma* are distinct from each other, whereas these foramina are usually confluent in the other subspecies (Ellerman and Morrison-Scott 1951). There is, however, considerable variation in the shape of the margins of the confluent foramina in *rufescens*. The single specimen from which *vultuma* was described appears to be an aberrant individual and the name should probably be considered a synonym of *rufescens*, as is *seiana*. Twelve other specimens from Baluchistan (but not the type locality) are typical of the Afghan pika *O. rufescens* in their confluent foramina.

Of the several subspecies of *O. rufescens*, the most distinctive is *O. r. regina* of the Kopet Dagh Mountains along the border between Turkmenia (USSR) and Iran, which averages considerably larger than other populations.

Status and Summary

In parts of its range the Afghan pika is considered a pest species because of the serious damage it inflicts on apple and walnut trees, wheat and other agricultural crops (Lay 1967, Khokhar and Fulk 1976, Roberts 1977, Khan and Smythe 1980, Khan 1981, Mian 1986, **Ahmad**, Hussain and Brooks 1987, Mian, **Tonsif** and **Ali** 1987, Mian, **Ali** and **Ali** 1988, Mian *et al.* 1988). In high plateau country in central Baluchistan, many narrow mountain valleys have been converted into farming areas. In higher valleys, apple orchards have increased in popularity as a cash crop and acreage has increased yearly. During winter months, when native vegetation is lacking, pikas forage on the trunks and branches of apple trees, sometimes debarking trees from 25-40cm above the ground. The amount of damage varies depending on the severity of the winter, but ranges from as little as 0.15% to 5.1% of trees killed. The proportion of trees partially damaged varies from 1.5% to 47.1% (**Ahmad**, Hussain and Brooks 1987). Because of these activities, the Afghan pika has been subject to control measures in Baluchistan.

This species has also been used to some extent in the fur industry (Vinogradov and Argyropulo 1941).

The race *shukurovi*, although isolated in the Great Balkhan Mountains, appears not to be threatened; its density varies between years, but in some years it can be found everywhere in these mountains (Sapargeldyev 1987). How-

ever, Sapargeldyev (1987) found a small isolated population of Afghan pikas on the Small Balkan Ridge, and it may well be endangered. The taxonomic status of this population is unclear because it lies between the ranges of two races: *shukurovi* and *regina*.

The Afghan pika is the only pika which has been "domesticated" as a laboratory animal, in France by Puget (1973, 1976) and in Japan (various investigators).

Description

During summer the Afghan pika has a distinct cream-colored collar which is outlined anteriorly and posteriorly with russet. The surface of the back and sides is gray-brown. The flanks and underparts are gray to dirty gray-white, commonly with a yellowish tinge. In winter the pelage is thick and uniformly brown; at this time the collar is only faintly noticeable, if at all. There are four pairs of mammae. The skull is large and usually moderately arched, but the degree of arching is variable. The interorbital region is relatively narrow with well-developed lateral crests present on both sides of the interorbital area in adults. The tympanic bullae are moderately large. There are no fenestrae present in the frontals. The diploid chromosome number = 60 (Vorontsov and Ivanitskaya 1973, Kimura, Nakatsu and Kikuchi 1984).

Distribution

The Afghan pika has a relatively patchy distribution in the mountains of southern **Turkmen** SSR, Soviet Union; Iran; Afghanistan; and Baluchistan, Pakistan. (See Fig. 3.2).

Habitat

The Afghan pika, like Pallas's pika *O. pallasi*, can best be considered to occupy an intermediate habitat type between that of the obligatory talus-dwelling and steppe-dwelling pikas. It is most often found in rocky desert situations, although it may make extensive burrow systems in fields devoid of stones (Ognev 1940, Vinogradov and Argyropulo 1941, Lay 1967, Hassinger 1973, Puget 1973, 1976, Roberts 1977, Fulk and Khokhar 1980, Sapargeldyev 1987). The Afghan pika may also be found in juniper forests (Roberts 1977). It frequently constructs burrows in adobe houses and walls such that they appear "completely perforated . . . like sponges" (Ognev 1940). Sapargeldyev (1987) determined that this species occupied habitats where the plant cover was no more than 30-60%; they do not occur in areas of higher percentage cover by plants.

E c o l o g y

Population densities reached by the Afghan pika may be as high as 70 animals per ha. Density may change markedly from year to year depending on weather conditions (Puget 1973, Fulk and Khokhar 1980, Sapargeldyev 1987).

In addition to eating a wide variety of commercial crops, Afghan pikas can subsist on a diversity of native xeric plants such as thistles (*Cousinia*), *Ephedra* and *Artemisia* (Ognev 1940, Lay 1967). Sapargeldyev (1987) lists 58 species of plants stored by this pika; the resulting **haypiles** weighed as much as

five kilogrammes. They collect stores of food twice per year: in spring before the rich vegetation becomes desiccated; and in autumn when the vegetation is again revived by rain (Ognev 1940, Roberts 1977).

The most important predator of the Afghan pika in southwestern Turkmenia is the levantine viper *Vipera lebitina*. The density of the viper appears dependent on that of the pika (Danov 1985).

Behavior

The Afghan pika is diurnally active. Unlike other diurnal pika species that have two peaks of activity (in the morning and in the evening during summer), there is only one morning peak of activity, presumably because the afternoon/evening temperatures throughout its range are very high.

The social organization of this pika is very labile and probably depends on when the annual summer drought occurs in any particular part of its range. In spring males live singly and their home ranges include those of several females (Ognev 1940, Sapargeldyev 1987). The first litter sometimes stays in the mother's shelter along with the second litter (Ognev 1940, Fulk and Khokhar 1980, Ivanitski, personal communication). Adult females and their offspring confine most of their activities to an area about 30m in diameter. Within this area the usual dispersion is of individual juvenile home ranges that significantly overlap each other and those of their parents. With the coming of the drought, however, the situation changes radically. At that time every pika protects its own small territory centered on its burrow.

Fulk and Khokhar (1980) reported that little to no aggression is expressed among residents of a family burrow system. Roberts (1977) noted that when animals were housed in captivity, they preferred to huddle together and showed no intraspecific aggression. On the other hand, N.A. Formozov (unpublished data) has observed that play behavior is a basic element of juvenile activity. Juveniles frequently box with one another and the duration of these bouts of activity are similar to those of Pallas's pika *O. pallasi pallasi*.

Vocal communication is not well developed in the Afghan pika and its repertoire is very different from that of other species (Kawamichi 1981, N.A. Formozov, unpublished data). The Afghan pika has no song (long call). It utters only a very weak melodious squeak and a peculiar prolonged cry (whistle) when alarmed. These vocalizations can only be heard for a very short distance (Ognev 1940, Roberts 1977). It is extremely rare for this species to use the alarm call in response to a terrestrial predator, although they do utter it regularly when avian predators or other large birds are detected (N.A. Formozov, unpublished data). Afghan pikas also can signify danger by drumming rapidly on the ground with their hind feet (Roberts 1977).

Neck glands are used to mark their territory by rubbing it against sticks and corners of stones. Two animals may do this simultaneously when they are in close proximity (N.A. Formozov, unpublished data).

Reproduction

The reproductive rate is high. Average litter size ranges from 5.2 (Fulk and Khokhar 1980) to 6.0 (Puget 1973 [captive animals], Roberts 1977) to 7.1 (Sapargeldyev 1987). Litters as large as ten or eleven have been reported (Fulk and Khokhar 1980, Sapargeldyev 1987). The breeding season may extend from mid-March to late September in some areas; individual females may produce as many as five litters during this time. In addition, young mature and breed in their summer of birth (Puget 1973, Fulk and Khokhar 1980).

Turkestan Red Pika

Ochotona rutila (Severtzov 1873)

Taxonomy

This monotypic species has generated little taxonomic confusion (Gureev 1964, Corbet 1978, Honacki, Kinman and Koeppl 1982, Weston 1982). Ellerman and Morrison-Scott (1951) included the forms *eythrotis*, *vulpina*, *gloveri* and *brookei* in the Turkestan red pika *O. rutila*. Here these forms are treated separately from *rutila*, as *O. eythrotis* (including *vulpina*) and *O. gloveri* (including *brookei*), on the basis of coloration, skull morphology and zoogeography (Ognev 1940, Gureev 1964, Weston 1982, Feng and Zheng 1985, Feng, Cai and Zheng 1986).

Status and Summary

This species is fairly rare in collections. However, there are currently no known threats to the distribution or abundance of the Turkestan red pika throughout its range.

Description

The summer pelage of the Turkestan red pika is rich rust-reddish dorsally with a more yellow cinnamon-buff tinge on the flanks. There is a broad yellowish white collar behind the ears and a dull rust-red transverse stripe on the chest. The ventral surface is whitish with a rusty tinge. In winter the coat is ash-gray with blackish-brown speckling. The skull is large and moderately arched with a broad and rather flat interorbital space. Fenestrae are not usually present in the frontals, except in Kirgizia and Tadzhikistan. The diploid chromosome number is 62 (Vorontsov and Ivanitskaya 1973).

Distribution

Ranges of the Tien Shan, Pamir, Kirgiz (= Alexander the Great), Gissar and other systems in Uzbek SSR, Tadzhik SSR, Kirgiz SSR and Kazakh SSR, Soviet Union; perhaps northern Afghanistan and eastern Xinjiang, China. Although Erbajeva (1988) stated that the Turkestan red pika is not known outside the USSR, both Büchner (1890) and Gureev (1964) specified that red pikas occurred in the western Kunlun and Nan Shan Mountains, where the red-eared pika *O. eythrotis* is known. However, according to modern records, the range of this species is completely allopatric to that of the



Talus habitat of Turkistan red pika *Ochotona rutila* in the Pamir Mountains, Tadzhikistan (Photo by Andrew Smith)

red-eared pika. One of the most important characteristics of the distribution of the Turkistan red pika is its extremely sporadic occurrence throughout its range. Within the Soviet Union it is only common in the vicinity of Great Alma-Ata Lake, Kazakh SSR and Iskander-Kul Lake, Tadzhik SSR. (See Fig. 3.5).

Habitat

Occupies scree and talus at moderate elevations in the mountains of Turkistan; these pikas normally do not occur at elevations higher than 3,000m even when talus habitat is available (Ognev 1940, Bernstein 1963, Sludski *et al.* 1980). The preferred talus habitat of the Turkistan red pika is very large stones; it chooses only the largest of these rocks for its shelter.

Ecology

The Turkistan red pika lives in family territories normally composed of an adult pair and, during the reproductive sea-

son, their offspring. Population density is low, normally 12-20 animals per ha (3.0-3.5 families/ha) (Bernstein 1963, Sludski *et al.* 1980). The distance separating centers of family territories is normally 50-100m, although they may be as close as 20-30m (Bernstein 1963). Population turnover, as determined by the percentage of yearlings in the population, was 65% per annum and longevity was three years (Bernstein and Klevezal 1965). Population levels tend to remain constant from year to year (Bernstein 1963).

This species caches food in the talus in a manner similar to most other pikas. Unlike most other talus-dwelling pika species, the Turkistan red pika does not forage in the open meadow any farther than two metres from the talus edge (Paskhina and Formozov, unpublished data). They mainly feed on little bits of turf between the stones. As the distribution of this vegetation on the talus is widely dispersed, home ranges are correspondingly large so that the pikas can find sufficient food.

During winter, voles *Clethrionomys frater* and *Alticola argentata* concentrate near and consume the food stores of pikas (Sludski *et al.* 1980). An important predator of the red pika is *Mustela erminea*; 19% of the scats of this species were found to contain fur of Turkistan red pikas (Sludski *et al.* 1980).

Behavior

Most social interactions are affiliative and occur within families. Young remain on their natal territory throughout much of the summer of their birth and feed on vegetation stored by their parents. Some, but apparently not all, juveniles overwinter with their parents (Bernstein 1963). Interactions between partners are normally expressed as long boxing sessions. During autumn the male and female partners are rarely seen together, although they maintain their mutual home range.

Although they are diurnal, activity is concentrated at dawn and dusk.

The Turkistan red pika is very quiet, in contrast to most pika species; it is commonly called the "silent" pika (Bernstein 1963, Formozov and Paskhina, unpublished data). It has no song, no typical pika alarm call and couples do not interact with loud signals. In alarm situations, this species escapes under rocks and makes a chattering call similar to that of the northern pika *O. hyperborea* and two subspecies of alpine pika *O. alpina scorodumovi* and *O. a. cinereofusca*. Conspecifics react to this signal by becoming alert. When members of a pair meet, they make long chirping sounds (Formozov and Paskhina, unpublished data).

Reproduction

The fecundity rate is low. Normally two litters averaging 4.2 young (range 2-6) are born during the spring to summer reproductive season. Young do not become reproductively active in their summer of birth (Bernstein 1964, Sludski *et al.* 1980).

Moupin Pika

Ochotona thibetana (Milne-Edwards 1871)

Subspecies: *Ochotona thibetana huangensis* (Matschie 1908) (includes *syrinx*); *Ochotona thibetana nangqenica* Zheng, Liu and Pi 1980; *Ochotona thibetana osgoodi* Anthony 1941; *Ochotona thibetana sacraria* Thomas 1923; *Ochotona thibetana sikimatia* Thomas 1922; *Ochotona thibetana thibetana* (Milne-Edwards 1871) (includes *hodgsoni*, *zappeyi*); *Ochotona thibetana xunhuaensis* Shou and Feng 1984

Taxonomy

In many treatments the Moupin pika *O. thibetana* has included the forms here assigned to the Gansu pika *O. cansus* (Allen 1938, Argyropulo 1948, Ellerman and Morrison-Scott 1951, Gureev 1964, Corbet 1978; Honacki, Kinman and Koepl 1982, Weston 1982). Although quite similar to *O. cansus*, here *thibetana* is separated on the basis of its skull characteristics and the observation that intermediate forms are not found in the extensive zone of sympatry between the two species (Feng and Kao 1974, Feng and Zheng 1985). Compared with *O. cansus*, *thibetana* has a longer skull and a wider zygomatic and interorbital width. Although Weston (1982) included *O. cansus* in *thibetana*, her morphometric analysis clearly shows the distinctiveness of the two forms.

The forms described as *O. lama* Mitchell and Punzo 1975 and *O. t. aliensis* Zheng 1979 were combined as *O. t. lama* by Feng, Cai and Zheng (1986). Here *lama* (*sensu* Feng, Cai and Zheng 1986), along with *Zhasaensis*, is combined with the nubra pika *O. nubrica* (see that account).

O. osgoodi Anthony was listed as a subspecies of the steppe pika *O. pusilla* by Ellerman and Morrison-Scott (1951), but was included in the Moupin pika *O. thibetana* by Corbet (1978) and Weston (1982). (It was not considered by Feng and Kao 1974.) Weston's morphometric analysis demonstrates its close phenetic similarity to *O. thibetana*. Following examination of the holotype (AMNH) and three additional specimens from near the type locality in Burma, we agree they are assignable to the Moupin pika *O. thibetana*.

Forrest's pika *O. forresti* Thomas 1923 was included in *O. thibetana* by Gureev (1964), Feng and Kao (1974), Honacki, Kinman and Koepl (1982) and Weston (1982). Here it is considered an independent species based on Feng and Zheng (1985) and our own study of the holotype (BMNH) and 16 additional specimens from Yunnan, Xizang, Burma, Assam, Bhutan and Sikkim.

Most authorities synonymise *O. hodgsoni* Bonhote 1904 and *O. zappeyi* Thomas 1922 with *O. t. thibetana* (Allen 1938, Ellerman and Morrison-Scott 1951, Weston 1982) and this listing is followed here. *O. syrinx* Thomas 1911c, 1911d was synonymised with *O. t. huangensis* by Allen (1938) and followed by Ellerman and Morrison-Scott (1951), Gureev (1964) and Weston (1982). However, Gureev (1964) also listed *huangensis* as a synonym of *daurica* (apparently a *lapsus calami*) and this allocation was followed without comment by Gromov and Baranova (1981). We have examined the holotype of *O. syrinx* (BMNH) and it is typical of *O. thibetana*, as are ten

other specimens from the type locality. They may represent a population isolated in the Tsing Ling Shan, where they are sympatric with *O. cansus morosa*. *O. t. sacraria* was synonymised with *O. t. thibetana* by Allen (1938), Ellerman and Morrison-Scott (1951) and Weston (1982), but was listed as a separate subspecies by Feng and Kao (1974) and Feng and Zheng (1985). Our examination of the holotype from Emei Shan, Sichuan, China (BMNH), as well as a series of 13 specimens from various localities in Yunnan assigned to this subspecies, leads us to agree that *sacraria* is correctly assigned to *O. thibetana* and we provisionally retain the subspecies.

Feng and Kao (1974), followed by Feng and Zheng (1985), placed *sikimatia* as a subspecies of the Gansu pika *O. cansus*, apparently because Thomas (1922) in his original description, compared *sikimatia* to *sorella*, a subspecies of *cansus*. They did not themselves examine any specimens of *sikimaria*. We have examined the holotype (BMNH) and a series of 19 additional specimens from Sikkim; all possessed the longer skull and wider zygomatic arch and interorbital region characteristic of the Moupin pika *O. thibetana* rather than *O. cansus*. We therefore assign *sikimatia* to the former species.

Throughout a broad area of southern Qinghai and northern Sichuan, the Moupin pika *O. thibetana* occurs in geographic sympatry with the Gansu pika *O. cansus*.

Status and Summary

The subspecies *O. t. sikimaria* may be endangered. R. K. Ghose (personal communication) has reported that there has been serious deterioration of its habitat in Sikkim, India. At the type locality (Lachen) human settlement, terraced cultivation, firewood collection and road construction etc. has resulted in an almost complete eradication of the thickets of rhododendron which were the preferred habitat of *sikimatia* in this region. Other affected endangered species in this area are the Himalayan langur *Presbytis entellus schistaceus* and red panda *Ailurus fulgens*. The subspecies *O. thibetana huangensis* may also be isolated in the Tsing Ling Shan, Shaanxi, China, and at risk due to habitat destruction.

This is a fairly common pika throughout most of its geographic range and other forms do not appear to be threatened; however we do not have accurate measurements on the consequences of deforestation throughout most of the range of the Moupin pika in southern China.

Description

The summer pelage is an overall dark russet-brown with some light speckling. The entire undersurface is tinged with ochraceous buff in most populations, but grayish in *O. t. huangensis*, and the throat collar is nearly russet. The general effect of the dorsal surface of the winter coat is buffy to dull brown. Distinguishing characteristics of the skull are given above. Although larger than *cansus*, this is also a fairly small pika (averaging a little more than 80g).

Distribution

Southeastern Qinghai, southern Gansu, southern Shaanxi, western Sichuan, western Hubei, western Yunnan, southern

Xizang, China; northern Burma; Bhutan; Sikkim, India. (See Fig. 3.8).

Habitat

A characteristic burrowing pika which occupies **mesic** bamboo and rhododendron forests at moderate elevations (as low as **1,800m**) (Allen 1938) to high elevation subalpine forests. Zheng (1989) reported that the Moupin pika also occupies rocky areas under forest canopies at an elevation of **2,400-4,100m**.

Ecology and Behavior

Unknown.

Reproduction

Litter size is from one to five ($N = 7$) (Feng and Kao 1974). A single specimen from Yulunshan Mountain (Yunnan Province, China) had two large embryos (Voronov 1963). Reproduction continues from at least April to July (Feng and Kao 1974).

Thomas' Pika

Ochotona thomasi Argyropulo 1948

Taxonomy

This monotypic species differs from all other known *Ochotona* and has not generated any systematic confusion (Argyropulo 1948, Gureev 1964, Corbet 1978, Honacki, Kinman and Koeppel 1982, Weston 1982, Feng and Zheng 1985). Thomas' pika *O. thomasi* is best regarded as expressing in extreme form the narrowing of the skull that is seen in the Gansu pika *O. cansus*; although the greatest skull length of the two species is similar (*cansus*, 33.3-35.3mm; *thomasi*, 33.6-35.5mm), the zygomatic width does not overlap (*cansus*, 15.4-16.4mm; *thomasi*, 13.5-14.8mm) (Feng and Kao 1974). *O. thomasi* is known to occur mainly in Qinghai and Gansu (one published record in northern Sichuan) where in many places it is **sympatric** with *O. cansus*; in contrast, it is not known to occur with the Moupin pika *O. thibetana*, although *thibetana* and *cansus* themselves are broadly sympatric (see accounts of those species).

The form described as *O. thibetana cilanica* Bannikov 1960 was synonymised with *O. thomasi* by Feng and Kao (1974); we have retained this assignment here.

Status and Summary

This is a rare species which has only been recorded from isolated mountains throughout its range. Its current population is unknown. The species may be in danger due to widespread control of other species considered to be "pest" vertebrates which occur throughout its range.

Description

The winter pelage of Thomas' pika is mouse-gray. The skull is very narrow and the profile of the braincase is elliptical in shape (Argyropulo 1948, Gureev 1964, Feng and Zheng 1985).

Distribution

Isolated mountain ranges from Gansu, Qinghai and Sichuan, China (See Fig. 3.7).

Habitat

This is a burrowing pika and is found in meadow thickets and rhododendron, *Salix* spp., *Caragana jubata* and *Dasiphora* (= *Potentilla*) *fruticosa* scrub (Zheng 1989). It lives primarily between 3,400 and 3,900m in elevation (Feng and Kao 1974).

Ecology

The ecology of Thomas' pika is essentially unknown. It may live in small widely spaced family groups. It is a diurnally active species (Zheng 1989).

Behavior and Reproduction

Unknown.

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Chapter 4: The Hares and Jackrabbits

John E.C. Flux and Renate Angermann

Status and Summary

The genus *Lepus* is very confusing taxonomically, with the number of recognized species varying from about a dozen to over 30, depending on the classification used. We adopt here a conservative approach and recognize 29 species. The eight subgenera proposed by various authors (*Allolagus*, *Boreolepus*, *Eulagos*, *Macrotolagus*, *Poecilolagus*, *Proeulagus*, and *Tarimolagus*) merely add to the confusion and are now usually ignored. The genus is widespread in both the Old and New Worlds, showing close parallel evolution of forms adapted to major habitats, eg. tundra (mountain hare *Lepus timidus*, arctic hare *L. arcticus*), steppe (European hare *L. europaeus*, white-tailed jackrabbit *L. townsendii*) and desert (Cape hare *L. capensis*, black-tailed jackrabbit *L. californicus*). The snowshoe hare *L. americanus* and European hare are very important game animals over much of North America and Europe, respectively, and many others are of regional importance. Most species favor open habitat and have benefited from habitat changes caused by traditional agriculture, but the recent trend to intensive chemical farming is having deleterious effects. Far more information is needed on the taxonomy and distribution of hares before clear conservation priorities can be established. In the meantime the best that can be done is to ensure the survival of distinct forms that appear to be limited to small distributional areas, such as the Tehuantepec jackrabbit *L. flavigularis* (recommended for endangered status); and the Hainan hare *L. hainanus*, black jackrabbit *L. insularis*, Manchurian black hare *L. melainus* and Ethiopian highland hare *L. starcki* (recommended for taxonomic and status surveys).

Physical Characteristics and Taxonomy

Hares (which include the snowshoe "rabbit" and jackrabbits of North America) are the most widespread lagomorph genus, occupying most of North America from 83°N to southern Mexico and nearly all the Old World, up to 70°N and including Africa. They are mainly open country grazers, relying on speed and staying power to elude their many enemies, and have consequently benefited from the great decline in forest cover caused by human populations. Only the snowshoe hare is an exclusively forest animal and its boreal habitat remains largely intact. Hares are classic species in following Bergmann's Rule; weights in the far north reach 5kg, most in temperate regions average 3kg, and those at the equator are about 2kg or less. There are, of course, exceptions like the



Snowshoe hare eating balsam fir (Photo by Len Rue, Jr.)

1.5kg snowshoe hare in the north and the large antelope jackrabbit *L. alleni* (3.6kg) in the deserts of Mexico. Apart from the two melanic forms, black jackrabbit and Manchurian black hare, all species have relatively similar "agouti" coloration in various shades of greyish brown on the back, with white or very pale buff below. Alpine or northern species turn white in winter, including the snowshoe hare, arctic hare, Japanese hare *L. brachyurus*, mountain hare and white-tailed jackrabbit. Hares have the longest ears and feet in the lagomorpha, associated with temperature control and their running ability, and the skulls are even lighter than those of rabbits. The groove on the front cutting edge of the upper incisors varies from a simple V to a complex branched structure filled with cement, possibly associated with the texture of the vegetation eaten, and is an important taxonomic character. The interparietal bone becomes fully fused with the parietals at an early age, although it is present as an aberration in some individuals and is commonly present in Abyssinian hare *L. habessinicus* and Cape hare. Growth rates of the precocious young are rapid and correlated with final body size, but this may be an artifact because large species live in colder regions where the summer is short and a fast growth rate is necessary (Flux and Jarvis 1970) or even because northern litters are larger, but the young are individually lighter after a shorter gestation period (Chapman 1984).

Despite some useful regional studies (Dixon *et al.* 1983, Robinson 1982, Schneider and Leipoldt 1983) the relationships between hares remain very confused and there is no

general consensus on the validity of many species. A major difficulty is that widespread species can show far more regional variation than is found between species that occur together, so early collectors tended to describe regional forms as new species and overlooked co-existing species, which can appear almost identical in the field (Flux and Flux 1983). The genus appears to have radiated recently, allowing the production of fertile hybrids between even the European hare and mountain hare (Gustavsson 1971). Most taxonomic characters show regional variation and even DNA analyses can reach completely conflicting conclusions (e.g. Palacios 1983, Schneider and Leipoldt 1983). Finally, natural changes in range following the ice ages, the recent expansion of agriculture and unrecorded translocations by hunters for at least 3,000 years have confused the picture even more: introduced populations can differentiate in body size in accordance with Bergmann's Rule within 100 years (Flux 1967a) and in color within 40 years (Bergengren 1969).

Given this uncertain taxonomy, it is scarcely surprising that the common ancestors and evolutionary pathways within *Lepus* are ill-defined. The only characteristic seemingly unique to hares, compared with other lagomorph genera, is the production of young born fully-furred, with their eyes open and ready to move within minutes (Corbet 1983). Their other characteristics (long legs, large hearts, dark muscle with myoglobin, wide air passage for breathing and a very **lightly-built** skeleton) are all physiological adaptations for sustained running and could be expected to arise independently in any lagomorph that took up this way of living. The earliest lagomorphs have been found in central Asia (Dawson 1981) and early leporines were widespread in both the Old and New Worlds before *Lepus* evolved. All hares have 48 chromosomes, but the banding patterns of the mountain hare and European hare are identical, while the two New World species, black-tailed jackrabbit and snowshoe hare, differ from the Old World pair in having two paracentric inversions (Van der Loo et al. 1981). This may indicate that speciation took place independently in the two hemispheres: as Hibbard (1963) suggested "The genus *Lepus* may be a composite group that may have arisen from both *pro-Sylvilagus* and *Oryctolagus* instead of from just one of the stocks." The arctic hares of both hemispheres, however, are closely related and many taxonomists regard them as conspecific. One recent view (Baker et al. 1983) suggests that the mountain hare crossed from Asia to the Canadian arctic and developed into the larger arctic hare form. Arctic hares later expanded back across the Bering Strait into Northeast Russia, where they appear to have remained distinct from the mountain hare. On the other hand, Dixon et al. (1983) found "few significant differences" between the Alaskan hare *L. othus*, arctic hare and mountain hare. In the black jackrabbit and some mainland forms like broom hare *L. castroviejoi* the parent stock is reasonably established, but there is as yet no good evolutionary picture of how *Lepus* has evolved as a whole.

Ecology, Behavior and Reproduction

With the exception of the forest-dwelling snowshoe hare, **Manchurian** hare *L. mandshuricus* and some populations of the mountain hare that occupy a similar forest niche in the Old World, the unifying aspect of habitats preferred by hares is open country. High arctic tundra, steppe, agricultural pasture, tropical savanna and desert are all occupied, but some form of cover (like shrubs, bushes or even rocks) is needed for protection from birds of prey. In peaty tundra without rocks the mountain hare survives by making burrows and desert hares may also burrow. Unlike rabbits, which run to cover for protection, hares tend to use cover for shelter by day and run into the open to avoid predators when attacked. Hares are entirely vegetarian, although some records of aberrant meat-eating exist for the snowshoe hare at extreme densities, when food is scarce. Many types of grasses, shrubs and forbs can be eaten and most hares are adaptable; thus the European hare in the New Zealand high country thrives in a flora without a single species in common with that of its ancestral home in Britain.

In keeping with their open habitats, hares range widely. Individual home ranges vary from 10 to 300 ha and often overlap on favored feeding areas. There is no indication of territorial behavior, although a hierarchy exists which affects access to food (Monaghan and Metcalfe 1985). Compared with the European rabbit, population densities are generally far lower and more uniform, averaging about one per 5-20ha, but dropping to 1/km² or lower for the mountain hare and arctic hare over much of their distribution. Again, the snowshoe hare is a well-known exception with a ten-year cycle of abundance and densities rising from about 0.1 hares per ha to 11-23 hares per ha at the peak (Keith and Windberg 1978). Because hares can travel a long way in a night to visit a good feeding ground, such as an alfalfa field, they sometimes give a misleading impression of high density. Hares appear to be essentially silent, solitary animals; but their behavioral interactions must be complex as they can regulate population density at levels normally far below the carrying capacity of the environment.

The preservation of large areas of open grassland habitat is one factor in the conservation of hare populations, but may not be the most important one. Hare species normally exclude each other from otherwise suitable habitat, the boundary between these disputed regions being decided by subtle differences in topography, cover, or predation. Thus the European hare in Scotland can occupy heather moorland, but only in the absence of the mountain hare, and mountain hares can occupy farmland if European hares are absent. In New Zealand, the European hare lives in typical mountain hare habitat on alpine grassland up to the snowline, and would doubtless be eliminated from this habitat completely if mountain hares were introduced. In Newfoundland the introduction of snowshoe hares was said to have resulted in the expulsion of the arctic

hare from the forest habitat it formerly occupied and its restriction to arctic vegetation above the tree line. Here subtle interactions with lynx were probably also involved, because the arctic hare could apparently compete successfully against snowshoe hares in the absence of lynx (Bergerud 1983). Whether arctic hares ever occurred in these forests has now been questioned, however (Hearn *et al.* 1987). In East Africa, the local distributions of Cape and African savanna hares *L. crawshayi* (= *L. victoriae*) depend on the history of fires because the African savanna hare prefers shrub cover and Cape hare more open habitat (Flux and Flux 1983). In America, the white-tailed jackrabbit is giving ground in the southwest to the black-tailed jackrabbit, which seems better adapted to the changed conditions following cultivation of the prairie (Dunn, *et al.* 1982). Clearly, in any conservation program for a species of *Lepus*, it will be important to understand the influence of competitors as well as the more usual factors of habitat and predators.

Habitat alteration probably has the single greatest impact on hare populations. For instance, the Hainan hare (endemic to Hainan Island, China) is reported to have suffered greatly from habitat alteration, in addition to hunting pressure (see Tang 1988). However, some evidence suggests that the scrub habitat preferred by the hares is actually increasing with deforestation (Song, personal communication). Populations of Chinese hare *L. sinensis* are presumably declining due to intensive agriculture throughout its range. Deforestation throughout the range of the **Manchurian** black hare has caused it to decline in numbers. Populations of most other leporids have probably been reduced, but their large distributional ranges have precluded any endangerment due to habitat disruption. Some species, such as Cape hare, may have increased in numbers and distribution because they favor grassland depleted by overgrazing with domestic stock. For the Indian hare *L. nigricollis* there are increasing reports of damage to forestry, agriculture and groundnut crops in India and Pakistan (Jain and Prakash 1976; Brooks, **Ahmad** and Hussain 1987), but it is not clear whether this is due to greater awareness of pests or a real increase in numbers. Certainly irrigation and the production of green crops in formerly desert areas is likely to provide more food for hares, and hence support higher populations, but the subsequent control demanded by farmers may then exterminate the animals over far wider areas.

The role of hares in community dynamics should be evaluated in relation to other **taxa** (especially rodents and other obligate grazing herbivores). We know of few investigations on this subject. Due to their differences in body mass and corresponding life history traits, it is unlikely that, in Asia for example, sympatric pikas *Ochotona*, hispid hares *Caprolagus*, and *Lepus* compete directly. Diffuse competition for forage may occur between them because of their reliance on similar vegetation. This subject is unstudied. However, species of *Lepus* tend to occupy different habitats in regions where they

overlap geographically. In north-central Kazakhstan, for example, mountain hare, European hare and Cape hare occupy mountain forest, steppe or agricultural land and desert, respectively (M. Erbajeva, pers. comm.). The hispid hare *Caprolagus* co-exists with Cape hare and Indian hare at Barnadi in northern India (Oliver, pers. comm.), probably occupying tall grassland, open country and shrubland respectively. In none of these cases, however, is it known to what extent the **sympatric** species may have been competing for resources.

The ecological position of *Lepus*, however, is by no means static; one species can successfully **compete** with another and exclude it from its former habitat if **ecological conditions** change. An example is the replacement of the mountain hare by European hare in several large forests in southern Byelorussia between 1964 and 1971. When hunting and changes to agriculture subsequently adversely affected the numbers of European hares, mountain hares re-invaded the forests and excluded European hares (Gaiduk 1983).

Hares can travel widely in the open when feeding and their effects on the vegetation, although selective, are consequently very difficult to measure. Thus, **Hewson** (1962) published a remarkable photograph of cotton grass flowering profusely in a hare-proof enclosure, while the surrounding country was almost devoid of flowers. Hares can be similarly most selective in eating grass seed-heads (Flux 1967b), but whether this curtails or increases the spread of these grasses will depend on the relative number of seeds digested or passed through the animal (Turcek 1966). African hares transport many species of plant seeds and burrs, which get caught in their fur (Agnew and Flux 1970) and Asian hares are probably equally effective. In desert areas in America, hares seek out plants with high nutrient levels and moisture content, so the soil water levels may be more important than the actual plant species in determining their diet (Hunter 1987). In other regions variation in phenol content of individual plants may determine which are eaten by hares (Haggman and Rousi 1985).

In hilly country, hares almost invariably descend to feed on the vegetation on valley floors and defecate while travelling to or from their daylight "forms" several hundred meters uphill. Thus hares actively reverse the normal downhill flow of nutrients in an ecosystem, a function performed by few other animals except raptors.

Breeding strategies in *Lepus* vary from one litter of six to eight young in the extreme north, to eight litters of one or two young at the equator, giving a surprisingly constant annual production of about ten young per female for most species (Flux 1981a). A notable exception is the arctic hare in Newfoundland with only three (Hearn *et al.* 1987). In comparison, cottontails vary in annual production of young from about 10 to 35 (Chapman, this volume) and *Oryctolagus* in New Zealand can average 45 (Gibb *et al.* 1985). The snowshoe hare is more variable than most hares in reproductive output, varying between areas and years from about 5.7 to 17.8 young per female per year (Keith 1981).

Economic Importance

The hares of Asia are of sufficient size to be hunted and serve as food for humans. In pre-revolutionary Russia, approximately six million skins of hares were sold annually by hunters. Before World War II, hares played an important role in the fur market. Mountain hare accounted for up to 6.1% and European hare for up to 5.6% of the total volume of the market (Ognev 1966). The numbers of hares taken was related to their abundance during the hunting season (Tomilova 1969). After World War II the number of hare skins sold by hunters to the State fur company dropped dramatically. For example, the number of tolai hare *L. capensis tolai* skins bought from hunters in Kazakh SSR in 1954 was 85,166. This total decreased to 5,015 in 1964, 425 in 1974, and finally to zero in 1975. This decline in the procurement of hare pelts is not related to their abundance in nature. Rather it is due to economics; the price of a hare skin has not changed there since the 1930s, thus hunters are not interested in selling them (Sludski et al. 1980). Sludski et al. (1980) estimate that 200,000 hares could be caught annually without harming the population in Kazakhstan. This stability of prices (in the face of rising inflation) had the same effect on other species in other regions. The total sale of European hare skins in 1932 was over three million. This total declined in 1954 to around two million and in 1966 to only 905,288 (Gruzdev 1974). This species also experienced severe epidemics in the 1960s that have been blamed for the decrease in number of pelts (Fadeev 1966). Today, the mountain hare is important for its fur only in Yakutia; this autonomous republic produces 50% of the total number of these skins sold annually in the Soviet Union (Popov 1973). Popov (1973) has noted that the cost of hare meat in the Soviet Union is roughly three times that of the skin. He has calculated that the meat from all hares caught in good years in Yakutia weighed as much as the meat from 50,000 cows, and in the Kama-Volga region it forms 60% of animal protein eaten.

In the Soviet Far East, the Manchurian hare is hunted very little (Krivosheyev 1984), which is fortunate because of the decline of this species in the face of deforestation of its habitat. In Mongolia, hare hunting has always been very limited. Bannikov (1954) wrote that only a few hundred mountain hares *L. timidus* and a few thousand tolai hares *L. capensis tolai* were collected annually. We suspect that this number is now reduced. The Mongolian people do not like the meat of hares and correspondingly do not hunt them. Very few tolai hares are caught by Kazakh people living in the Mongolian Altai Mountains; their primary use of these animals is for feeding their hunting golden eagles *Aquila chrysaetos*. In the European part of the Soviet Union, hares remain important game in sport hunting, but the number of hares caught for this activity is difficult to determine. At least five farms of 500-1,000 km² have been established in the Ukraine to breed hares for export to western Europe (Radchuk 1963).

Each year from 1958 to 1981 about 10,000 Yarkand hare *L. yarkandensis* have been harvested without decline, in spite of

its restricted range (Gao 1983). Its preferred wasteland habitat continues to be available because farmers rotate land after cropping. However, hunting of Hainan hares has contributed to the possible decline of this species on Hainan Island, China. They are still being hunted and snared by the indigenous Li people and are sold in the local market at 3 yuan each. Although they are not protected (even in reserves), and hence occur at very low densities, the overall numbers may be stable or even increasing because the area of suitable habitat (scrub covered hills) has been increasing as the forests are cleared (Song, personal communication). Around Beijing, China, populations of the tolai hare have declined so much over the past ten years that in 1989 a closed season was declared to conserve stocks. Most hares in this region are shot, but some are hunted with hawks. The decrease in abundance has been attributed to the increase in intensive agriculture and use of insecticides in the region (Gao, personal communication). We have no data on the use for skins or food of other *Lepus* throughout China. In Korea special hunting regulations have been suggested to allow farmers to catch hares for food and prevent damage they cause to barley and fruit trees (Howard et al. 1975). In Japan 500,000 Japanese hares are shot per year by 140,000 hunters, and many more are killed to prevent damage to forestry plantations (Kuroda 1953).

At least one control program directed at a rodent has had a detrimental affect on a hare population. In southwestern Transbaikalia (Chitinskaya Oblast), Soviet Union, tolai hares have become very rare near the 50th parallel. The reason for this population decline is the extermination in the area of Mongolian marmots *Marmot sibirica* by the anti-plague station in this district. The hares use the burrows of marmots for shelter and rest, especially during their breeding season. The lack of shelters provided by marmots has apparently reduced the number of hares here, although in other areas as the Turkmen SSR "this species does not use burrows" (Ishadov 1974).

Conclusion

Our present knowledge on hares is in many respects insufficient and progress is too slow. If we really wish to achieve something (which is essential as a precondition of conservation attempts) we must encourage and sponsor research on hares:

1. to clarify existing taxonomic problems
2. to clarify the precise geographic distribution of species
3. to collect field data on the abundance, habitat requirements and biology of the species

As we cannot expect to get fresh material from the vast areas of Africa and Asia in the near future, one important step towards items 1) and 2) would be a careful revision of the

world's largest museum collections (many museum labels or literature data cannot be trusted, hence reliable distribution data will be obtained only after re-identifying museum specimens). However, because of the diagnostic problems with hares, this task can only be successfully undertaken by people who have considerable experience in the taxonomy and diagnosis of hares and rabbits - otherwise one would only add to the existing confusion. From long experience of the subject, we find that many divergent views on hare taxonomy result from a too local perspective, which leads to splitting. One can not judge on hare taxonomy without taking into account the enormous geographic variability found in this genus.

Species Accounts

Antelope Jackrabbit *Lepus alleni* Mearns 1890

Subspecies: *Lepus alleni alleni*; *Lepus alleni palitans*; *Lepus alleni tiburonensis*

Taxonomy

Hall (1981) recognizes three subspecies: *L. a. alleni* from South Arizona to about 28°N in Sonora; *L. a. palitans* further south in Sinaloa; and *L. a. tiburonensis*, which is restricted to Tiburon Island in the Gulf of California.

Description

The antelope jackrabbit is one of the largest North American hares, averaging **3.63kg** (2.7-5.9) in Arizona (Vorhies and Taylor 1933). It is a pale, sandy-colored animal. The black ear-tips present on most hares are lacking and white extends from the undersurface well up its sides, as indicated by its alternative name of white-sided jackrabbit. In keeping with its desert habitat, the ears are very long: 162mm (138-173), as are the hind feet: 140mm (127-150). No sexual dimorphism is recorded.

Distribution.

According to Dunn *et al.* (1982) the distribution of the antelope jackrabbit has not changed markedly since 1959. It occupies the lower Sonoran life zone (from sea level to **1,200m**) in south Arizona and a coastal strip of northwest Mexico, **100-300km** wide, south to 22°N. Marginal records for Arizona are: 35 miles East of Florence; Cascabel; 7 miles North of Fort Huachua; Casa Grande; and Queen Creek (Cockrum 1961), and there is one record for Yuma County (Simmons 1966). (See Fig. 4.1).

Habitat and Ecology

The classic study by Vorhies and Taylor (1933) on the Santa Rita Experimental Range in southern Arizona still provides the only detailed information for this species. Its preferred habitat is grassy slopes at moderate elevation and the cactus belt, creosote bush desert and valley bottoms. Densities are

highest (0.53 hares/ha) on mesa type vegetation, in contrast to semi-desert for the black-tailed jackrabbit *L. californicus* in the same region. Where food and shelter are separated, daily movements occur, and ten mile round trips from desert to feed on alfalfa are known. "We frequently see groups of from 2 to 6 individuals . . . as an example of concentration . . . 17, and again 25 antelope jackrabbits in one bunch" (Vorhies and Taylor 1933: p482). The home range probably varies greatly with habitat: "several miles in diameter" or within a 500ft square area. Fresh grass is eaten after the two rainy seasons, mesquite and cactus in the dry season. Throughout the year, the antelope jackrabbit consumes 45% grass and 36% mesquite, compared with 24% and 56% respectively, for black-tailed jackrabbit in the same region (Vorhies and Taylor 1933).

Behavior

The antelope jackrabbit is nocturnal and feeds mainly in the evening and early morning. They are silent except for the usual distress cry, grunts and "chuck" calls. Mating is promiscuous; males chase females, and box to repel rivals. There are many more forms than jackrabbits, and the same individual was noted at the same form at least three times (Vorhies and

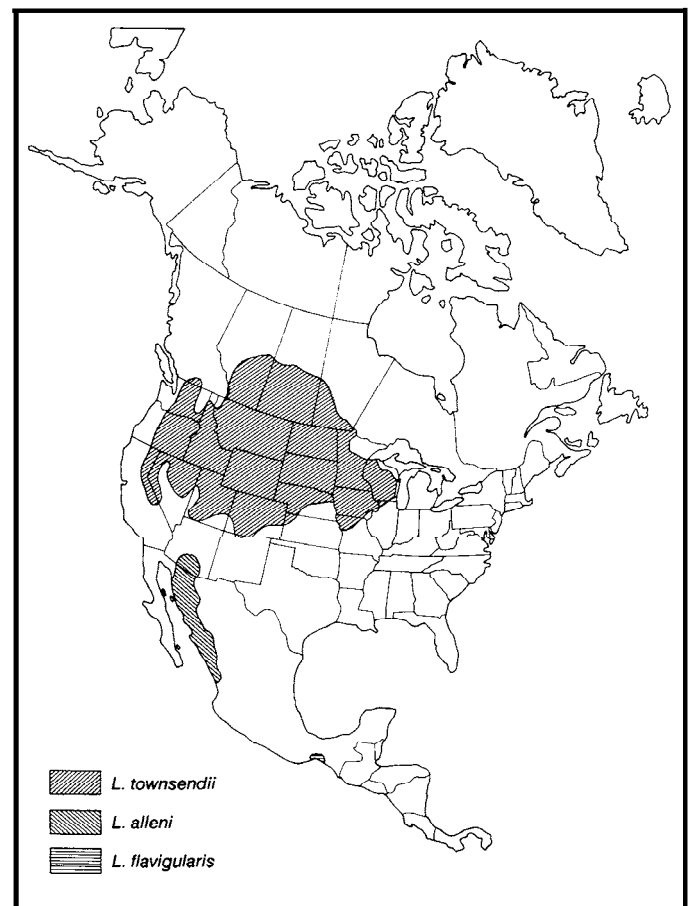
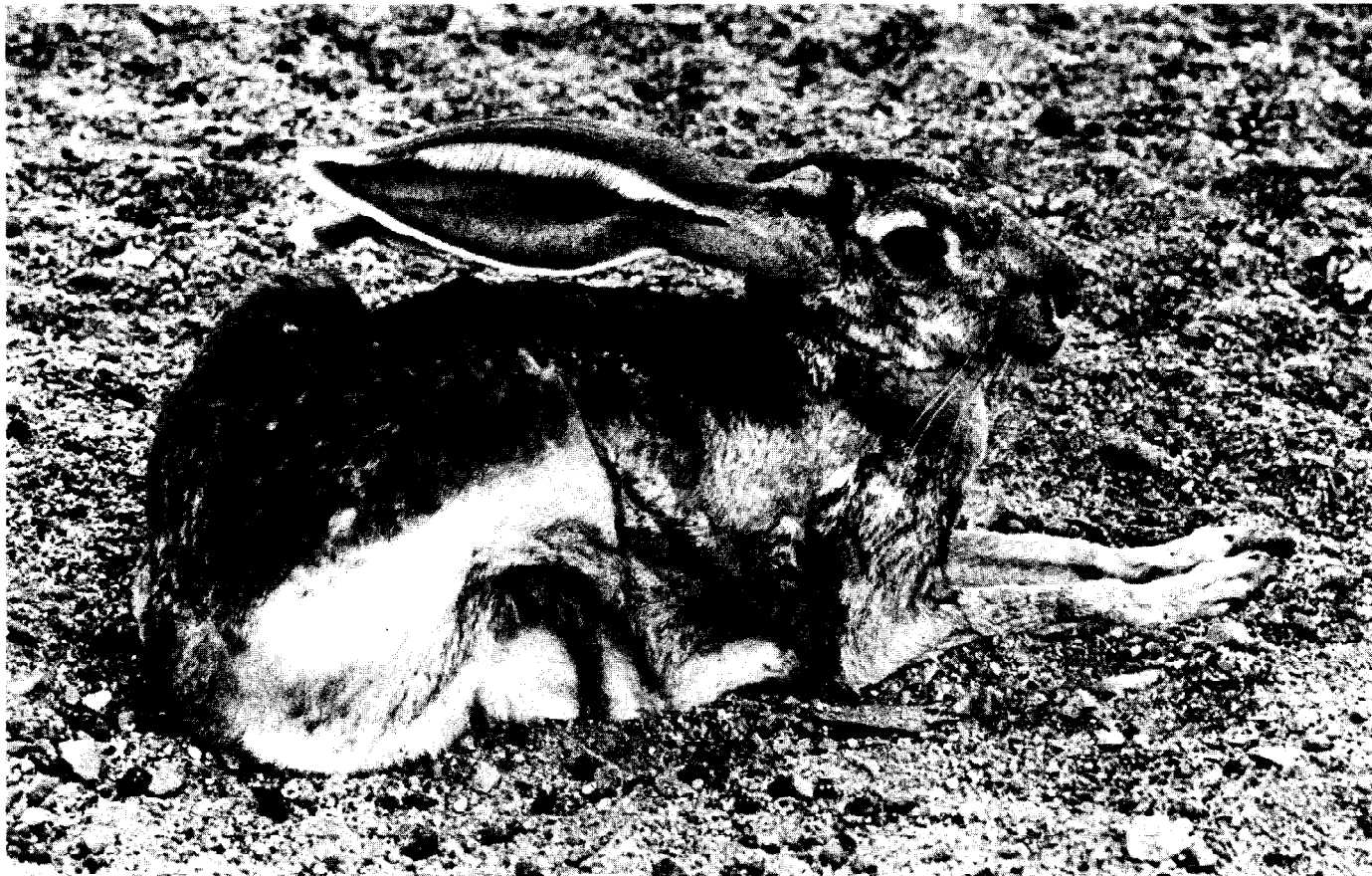


Figure 4.1 Distribution of the antelope jackrabbit *Lepus alleni*, Tehuantepec jackrabbit *L. flavigularis* and white-tailed jackrabbit *L. townsendii* in North America



Antelope jackrabbit *Lepus alleni* (Photo by Leonard Lee Rue III)

Taylor 1933). A dominance hierarchy as in other *Lepus* is likely, but there is no recent work on behavior. The white skin over the sides and rump is pulled up by special muscles to present a “flash” display to following predators; this escape behavior is shared only by the white-sided jackrabbit *L. callosotis*.

Reproduction

In Arizona breeding was reported in every month except November; but the percentage of females pregnant showed peaks correlated with rainfall, as did the litter size which varied from about 1.5 to 3.1, the mean being 2.1 (range 1-5) (Vorhies and Taylor 1933). The age of maturity is uncertain, but females probably breed within a year of birth.

Status and Summary

Populations of the antelope jackrabbit appear stable and do not cycle as some northern species do. With overgrazing by stock and the consequent decline in pasture-cover, the antelope jackrabbit is likely to give way to the black-tailed jackrabbit which thrives on such conditions. They are regarded as a common non-game mammal in Arizona where they are often hunted at the same time as black-tailed jackrabbits as a pest on stock range, with no close season or bag limit (Dunn et al. 1982). Their status in Mexico requires investigation.

Snowshoe Hare

Lepus americanus Erxleben 1777

Subspecies: *Lepus americanus americanus*, *Lepus americanus bairdii*, *Lepus americanus cascadiensis*, *Lepus americanus columbiensis*, *Lepus americanus dalli*, *Lepus americanus khamathensis*, *Lepus americanus oregonus*, *Lepus americanus pallidus*, *Lepus americanus phaeonotus*, *Lepus americanus pineus*, *Lepus americanus seclusus*, *Lepus americanus struthopus*, *Lepus americanus tahoensis*, *Lepus americanus virginianus*, *Lepus americanus washingtonii*

Description and Taxonomy

The rabbit-sized snowshoe hare is the smallest *Lepus*, averaging 1,300g with different populations ranging from about 1,050g to 1,600g (Bittner and Rongstad 1982). The ears are relatively small (62-70mm) but the hind feet are very big (112-150mm) (Hall 1981). In summer the upper fur is brownish, dusky grey, or even rusty; the belly, underchin, and sometimes the feet white. In winter most populations moult to a white coat, although the under fur remains grey and the white is restricted to the tips of the hairs. Two subspecies (*L. a. oregonus* and *L. a. washingtonii*) may retain the summer coat coloring in winter.

Taxonomically the snowshoe hare is very distinct from

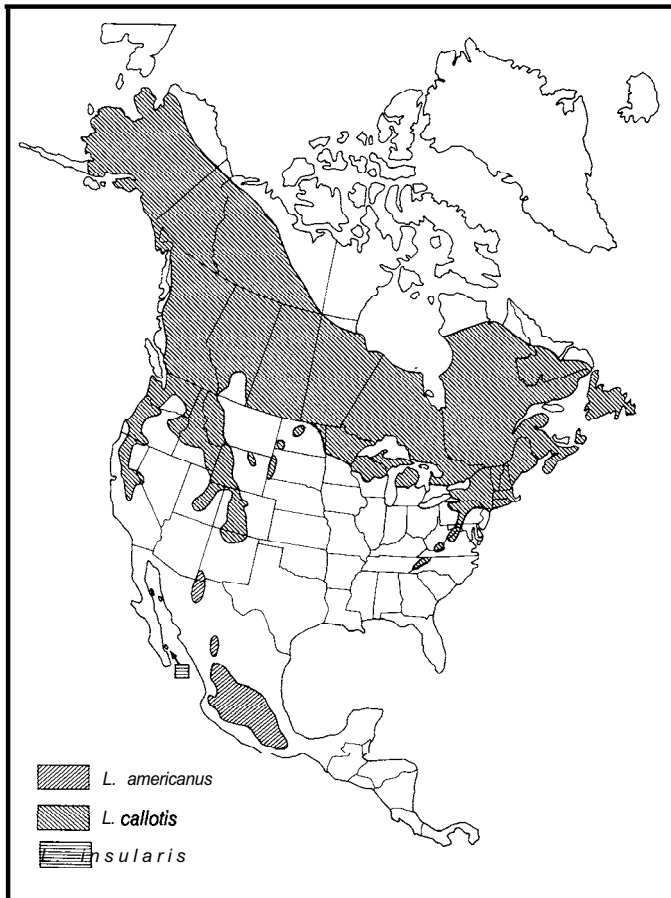


Figure 4.2 Distribution of the snowshoe hare *Lepus americanus*, white-sided jackrabbit *L. callotis* and black jackrabbit *L. insularis* in North America

other *Lepus*, in size, proportions, and coloring, as well as in behavior and habitat requirements. The distributions of the fifteen subspecies (see Hall 1981) show most subspeciation is in America and probably took place in ice-age refugia; the two subspecies which occupy practically the whole of Canada (*L. a. americanus* in the east, *L. a. dalli* in the west) presumably followed the retreating ice. However, Nagorsen (1985) considers most of the variation is clinal and follows climatic boundaries, and he sees little merit in recognizing any subspecies in the snowshoe hare.

Distribution

The snowshoe hare is the most widespread of all New World hares, extending from Alaska to Newfoundland, and penetrating far south into America down the Coastal Range, the Rockies, and the Appalachians, to mid California, northern New Mexico and Tennessee. On open tundra in the far north of Canada it gives way to the arctic hare *L. arcticus*. South of the conifer belt, its main stronghold, it may occupy mixed hardwood, cut-over forest, and swamps. The snowshoe hare seems reluctant to cross open country and is not found as a relict species in small isolated patches of forest (Lomolino *et al.* 1989). (See Fig. 4.2).

Habitat and Ecology

Given their enormous geographic range, it is not surprising that snowshoe hares use a wide range of forest types: conifers, aspen, birch, beech, maple and mixed hardwoods. They show a marked preference for subclimax forest, transition zones, and swamp edges; hence fires are important modifiers. Peak numbers follow fire when the scrub and regrowth become dense, then as the forest matures and the ground cover becomes over-shaded, numbers decline.

The home range is smaller in thick cover, averaging 5.9-13ha in different studies (Bittner and Rongstad 1982). Males have larger ranges than females, and juveniles have smaller ranges than adults (Adams 1959). Populations cycle, with peak densities every eight to eleven years up to 300 times higher than the troughs, but the normal range is 10- to 30-fold (Keith 1981). Cycles are synchronous over wide geographic regions. At peak numbers (31/ha in Alberta, Keith and Windberg 1978) snowshoe hares have an enormous effect on the vegetation and predators in their habitat. The food eaten changes from grasses, sedges, dandelions and various herbs in summer, to birch, spruce, willow, tamarack, and pine in winter. At population peaks, aspen and willow may be badly ring-barked by snowshoe hares; the ensuing scarcity of food has been suggested as a primary trigger of the cycles, which are then amplified by the effect of predators (Keith 1983). Other studies found no shortage of food and suggest that predation may be the only cause (Sinclair *et al.* 1988) .

Behavior

Good descriptive accounts of snowshoe hare life history and behavior are given by Grange (1932, 1957) and Adams (1959) and behavioral development by Nice *et al.* (1956). Snowshoes are nocturnal, use forms for cover by day and make regular runways to reach favored feeding areas. The mating behavior is promiscuous, with males involved more frequently and in more intense interactions than females (Graf 1985). There is a clear dominance hierarchy at feeding stations and in the wild. Males are more dominant in winter and females in summer during the breeding season. Leverets gather at a nursing place one to two hours after sunset and suckle as soon as the female arrives for two to five minutes. (Graf and Sinclair 1987). Considering the importance of behavioral interactions in relation to population cycles, it is surprising that there is no detailed description of behavioral changes during a complete cycle.

Reproduction

The breeding season is primarily controlled by day length, but the effect of weather and phase of the population cycle can alter the date of the first litter by three weeks in Alberta (Cary and Keith 1979). Two litters a year are normal in the far north and in the south at high altitudes; in central parts of its distribution three or four litters are produced (Keith 1981). Total production per year per female ranges from 5.7 to 17.8. Litter size increases by about one from the first litter of the season to later litters, and regionally from about 2.2 to almost six (Keith 1981).

Status and Summary

According to Rapoport (1982) the total biomass of the snowshoe hare in North America (2.7 million tons) is almost as high as that of the cottontail *S. floridanus* (2.9 million tons) and more than one million tons higher than the biomass of any other *Lepus* in the region. The snowshoe hare is clearly a most important animal, as game, as a pest of forestry and as a major component of the ten year cycle, indirectly and directly affecting the food supply and number of predators present in their ecosystem.

Arctic Hare *Lepus arcticus* Linnaeus 1758

Subspecies: *Lepus arcticus andersoni*, *Lepus arcticus arcticus*, *Lepus arcticus bangsii*, *Lepus arcticus banksicola*, *Lepus arcticus groenlandicus*, *Lepus arcticus hubbardi*, *Lepus arcticus labradorius*, *Lepus arcticus monstrabilis*, *Lepus arcticus porsildi*, *Lepus arcticus tschuktschorum*.

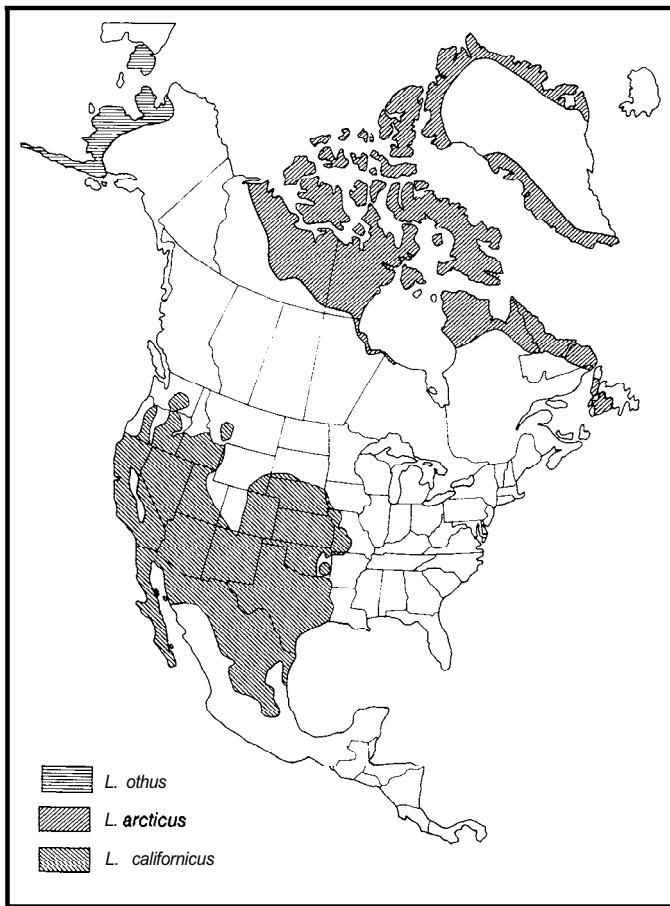


Figure 4.3 Distribution of the Arctic hare *Lepus arcticus*, black-tailed jackrabbit *L. californicus* and Alaskan hare *L. othus* in North America



Arctic hares *Lepus arcticus* on Axel Heiberg Island, Canada
(Photo by G. R. Parker)

Description and Taxonomy

Arctic hares are large, compact animals weighing 4-5kg. Traditionally three species were recognized: *L. othus* in Alaska, *L. arcticus* in northern Canada and Greenland, and *L. timidus* in the Old World. Because they form a circumpolar "ring species" some authorities consider them all *L. timidus*. There is also the view suggested by Baker *et al.* (1983) that two species are recognizable: *L. timidus* in the Old World; and the large form *L. arcticus* in Greenland, Northern Canada, Alaska and the Chukot Peninsula, Soviet Union. The hares of the Chukot Peninsula are the same size as *L. othus* in Alaska, and far larger than adjacent populations of *L. timidus* (Angermann 1967a). Under this classification there are 10 subspecies of the arctic hare.

Distribution

The arctic hare appears to be excluded from boreal forest by the snowshoe hare *L. americanus* (or the latter's associated predators like the lynx, Bergerud 1983). It occurs on circumpolar open tundra from Greenland to the Chukot Peninsula, but with a gap in its range along the north of Alaska, reaching 83°N in Ellesmere Island and Greenland (Baker *et al.* 1983). Many of the islands it inhabits are accessible across the ice in winter. (See Fig. 4.3).

Habitat and Ecology

The arctic hare inhabits tundra north of the tree line, an extremely bleak habitat subject to continuous darkness for several weeks in winter. They favor hillsides or rock-strewn plateaux rather than flat bogland (Macpherson and Manning 1959), using rocks for cover from aerial predators and occasionally from foxes and wolves if hard pressed. In summer, meadows of grasses, sedges, *Dryas*, and willow are favored and in winter arctic willow can form up to 95% of the diet (Parker 1977). Snow cover and exposure to wind are also important, with hares in herds of several hundred moving from one location to another in search of food in winter.



Habitat of Arctic hare *Lepus arcticus* in the barrens of Newfoundland, Canada (Photo by Dan Keppie)

On Axel Heiberg Island a herd of 250-300 hares spent the winter moving over about 35km² (Parker 1977) so the concept of home range is hard to apply to this species. In summer the hares spread out to breed. Peak densities appear high because these hares are large and often very conspicuous, with white coats against a snowless background, but vast areas may have no hares at all and numbers vary from year to year (Gould 1988). On Banks Island, Manning and Macpherson (1958) estimated about 100-200 hares lived on five square miles of suitable valley near Sachs Harbor, and on Kugong Island where they were commonest they found 0.5/square mile. In Newfoundland, Hearn, Keith and Rongstad (1987) recorded one hare/km², but a population introduced in 1969 on Brunette Island reached a density of about 1/ha within ten years.

Behavior

Adult hares in summer sit in shallow forms on gravel ridges or slopes, often close to a large rock for cover. The young are well camouflaged and are very hard to see even in the open when they squat flat. They are fed by the mother at 18 hour intervals, with suckling bouts lasting only 79-128 seconds (Burton 1989). Flocking behavior (otherwise found only to a minor degree in the mountain hare *L. timidus*) is very characteristic: "They travel as one ... all change direction at the same time. They're synchronized" (Brandenburg 1988). In the Canadian high arctic they run from predators on their hind feet, upright like a kangaroo, but it is not clear how widespread this behavior is and it has not been reported for the mountain hare. When young hares reach about half adult size they gather in juvenile herds of up to 20 at first, which the adults join later (Parker 1977). They are usually extremely tame and allow close approach, although herds of young hares may become very wild if a wolf attacks, running two kilometres. Little is known of their behavior in winter, when herds may follow musk oxen to graze on plants kicked free of snow (Parker 1977).

Reproduction

In the far north there is only time for a single litter each year, ovulation taking place in early May and the first young being seen towards the end of June (Parker 1977). The average litter size on Axel Heiberg Island was about five, although litters of eight have been recorded by Manning and Macpherson (1958) and Burton (1989) on Banks Island and Ellesmere Island respectively. In Newfoundland the average litter size was 3.0 (Hearn, Keith and Rongstad 1987), but in some years two litters may be produced.

Status and Summary

Although there is some hunting of arctic hares, most populations live in areas that are still extremely difficult to reach. Over much of its range densities are so low that they appear to be at risk, yet there is no evidence that this situation is abnormal or that it has changed in historical times, even in relatively accessible areas like Newfoundland. Their high densities on small islands free of competitors and predators indicates a good conservation technique should it ever be necessary. Study of communication between individual hares at low density would be useful to understand population dynamics in this species, and the disruptive effect of aircraft and snowmobiles should be assessed as tourism increases.

Japanese Hare

Lepus brachyurus Temminck 1845

Subspecies: *Lepus brachyurus angustidens*, *Lepus brachyurus brachyurus*, *Lepus brachyurus lyoni*, *Lepus brachyurus okiensis*

Description and Taxonomy

The Japanese hare is a relatively small species (about 2.5kg), in general appearance very similar to the mountain hare *L. timidus*. Several color forms are recognized, varying from dark brownish-grey to reddish-brown, with variable amounts of white on the head and legs (Imaizumi 1970). *L. b. angustidens* has five colour phases and *L. b. brachyurus* four colour phases. Northern subspecies turn white in winter.

Distribution

The Japanese hare occurs on the main islands of Japan, except Hokkaido, in fields and open forest from sea level to 2,700m (Fig. 4.4). *L. b. angustidens* is restricted to the northwestern half of Honshu, *L. b. brachyurus* to the southeastern half of Honshu, Kyushu and Shikoku, *L. b. lyoni* to Sado Island and *L. b. okiensis* to the Oki Islands. Although hares have been important game (for falconry), there seems to have been little transport of hares for liberation, to judge from the continued existence of so many color forms. *L. b. okiensis*, however, does not turn white in winter despite heavy snowfall on the Oki Islands, so may be a relatively recent introduction. (See Fig. 4.4).

Habitat and Ecology

The Japanese hare occupies open fields and thin forest from the lowlands to the alpine zone (Imaizumi 1970). Because traditional forms of agriculture and land use have remained stable for many centuries and 68% of Japan remains in forest, hare habitat has probably likewise remained stable, allowing the formation of geographical color forms.

There is little information on home range, but Hayashi (1978) estimates the population density of *L. b. angustidens* on Honshu at 0.4/ha. The food in winter includes leaves and bark of young trees, especially cryptomeria, maple, paulownia, *Acanthopanax*, *Aralia* and Leguminosae; in summer, grasses (48% of the diet - Horino and Kuwahata 1984), pulse, *Stellaria*, *Polygonum* and grain (Otsu 1973). This causes some damage to plantation forestry and fruit trees (Yamada and Isagi 1988).

Behavior

In captivity, the Japanese hare is nocturnal, becoming active at about 19.00 hr and retiring to a form at 07.00 to 08.00 hours after a period of restless running (Tachibana, Kamikawa,

Jyogo and Yamamura 1970) which "may correspond to the alerting behavior well-known among hunters for the hares before entering their resting sites". Hares often closed their eyes for one to three minutes, a total of about 20 minutes per day. Grooming took place before and after activity. Young hares normally suckle once or twice a night (13% three times) for durations of less than three minutes, mostly between 22.00 and 02.00 hours (Yamada *et al.* 1988).

Reproduction

The breeding season extends from February to July with young born between April and August, mostly in May and June when litter size is also largest. The litter size averages 1.9 (2.5 in May), maximum four (Otsu 1965) and females become sexually mature at ten months. The weight at birth for two young averaged 132g (Yamada, Shiraishi and Uchida 1988).

Status and Summary

The Japanese hare is an important game animal, with about 400,000-800,000 being caught each year, the average having increased from about 500,000 in 1925 to 700,000 by 1965 (Imaizumi 1970). Damage to forest plantations and fruit trees is also significant. There is no indication of decline in population at present.

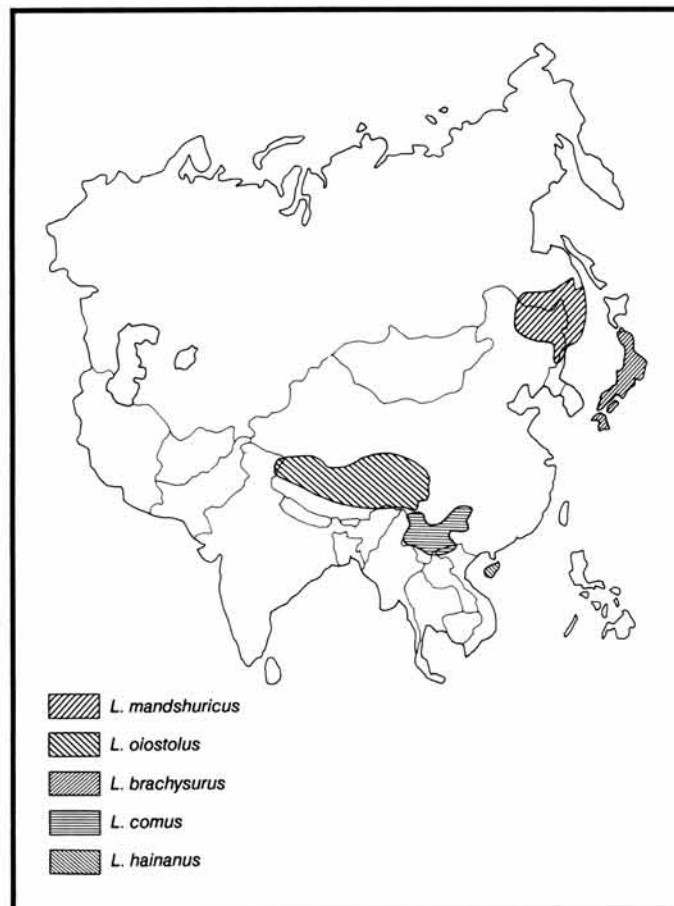


Figure 4.4 Distribution of the Japanese hare *Lepus brachysurus*, Yunnan hare *L. comus*, Hainan hare *L. hainanus* Manchurian hare *L. mandshuricus* and woolly hare *L. oiostolus* in Asia

Black-tailed Jackrabbit *Lepus californicus* Gray 1837

Subspecies: *Lepus californicus altamirae*, *Lepus californicus asellus*, *Lepus californicus bennettii*, *Lepus californicus californicus*, *Lepus californicus curti*, *Lepus californicus deserticola*, *Lepus californicus eremicus*, *Lepus californicus festinus*, *Lepus californicus magdalenae*, *Lepus californicus martirensis*, *Lepus californicus melanotis*, *Lepus californicus merriami*, *Lepus californicus richardsonii*, *Lepus californicus sheldoni*, *Lepus californicus texianus*, *Lepus californicus wallawalla*, *Lepus californicus xanti*.

Taxonomy

There are 17 subspecies according to Hall (1981), which fall in two groups separated by the Colorado River. A conservative view would use *L. c. californicus* for the western populations and *L. c. texianus* for the eastern ones (Dixon *et al.* 1983).

Description

The black-tailed jackrabbit is a lean, long-legged hare of about 2.5kg (1.3-3.1kg), with long ears (100-130mm) and a relatively long tail. The black upper surface of the tail extends as a line on the rump, and is the simplest way of distinguishing this hare from the white-tailed jackrabbit *L. townsendii*. The lack of much white on the sides and black tipped ears separates it from the antelope jackrabbit *L. alleni*. The coat color is greyish-brown to sandy, matching its desert or dry grassland habitat (Fig. 4.3).



Black-tailed jackrabbit *Lepus californicus*
(Photo by Leonard Lee Rue III)

Distribution

The black-tailed jackrabbit has a wide distribution in the arid Southwest of America, extending from Washington and South Dakota to Baja California and north Mexico, and from the Pacific coast almost to the Mississippi. Because it adapts well to overgrazed range (Vorhies and Taylor 1933) this species seems to be expanding at the expense of the white-tailed jackrabbit in the Northeast and the antelope *L. alleni* and white-sided *L. callotis* jackrabbits in the south. There are successfully introduced populations in South Florida, Massachusetts, Virginia, Maryland and New Jersey. (See Fig. 4.3).

Habitat and Ecology

The black-tailed jackrabbit favors arid regions and areas of short grass rangeland, from sea level to about 3,800m. Many different vegetation types are used, including sagebrush-creosote bush, mesquite-snakeweed, and juniper-big sagebrush (Dunn *et al.* 1982). According to Flinders and Hansen (1975), where the black-tailed jackrabbit and white-tailed jackrabbit co-exist, the former displaces the white-tailed jackrabbit onto higher, more sparse vegetation and can out-compete it in adaptability to a wider range of habitats. They also occur on agricultural land in California where they can be a pest of crops and fruit trees (Lechleitner 1958).

Black-tailed jackrabbit home ranges in California averaged 20ha, with the unusual feature that females had larger ranges than the males (Lechleitner 1958). In Idaho and Kansas, home ranges averaged 16ha (French, McBride and Detmer 1965, Tiemeier 1965). Home range size doubtless varies with population density, which varied in a six to ten year cycle in N. Utah from 0.1-1 hare/ha (Gross, Stoddart and Wagner 1974). Similar densities were recorded in Arizona (1.2/ha - Vorhies and Taylor 1933) but on agricultural land Lechleitner (1958) recorded 2.7/ha and Bronson and Tiemeier (1959) 1.5-2.5/ha, with local concentrations as high as 34.6/ha at night on an isolated wheatfield.

As in most hares, the diet changes from predominantly grasses and sedges in summer, to shrubs in winter or in dry seasons in desert areas (Flinders and Hansen 1972).

Behavior

Black-tailed jackrabbits are nocturnal and generally solitary, although at high densities many may converge on favored food such as winter wheat. In deep vegetation a jackrabbit may attempt to sneak away from an intruder unseen; the usual response is to "freeze" and jump up suddenly when it knows it has been seen (Lechleitner (1958). Aggressive behavior between males, and between females rebuffing males, is normally limited to sexual chasing in the mating season (Pontrelli 1968). By day the hares rest under bushes for shelter, but in the Mojave Desert, Nagy, Shoemaker and Costa (1976) found black-tailed jackrabbits made or enlarged short burrows for protection from the sun.

Reproduction

The breeding season increases from 128 days in South Idaho to about 300 days in Arizona, so the potential number of litters likewise increases, from about three to seven. The litter size varies inversely from 4.9 in the north to 2.2-1.8 in the south, giving a total output per female per year of about 10-15 (Feldhamer 1979). Litter size increases from a small first litter to a peak in the middle of the breeding season and then declines (Lechleitner 1959). Early-born females may breed in their year of birth (Gross *et al.* 1974).

Status and Summary

In the late 1800s enormous numbers of jackrabbits were killed

by farmers to protect crops, and some were sold to markets in the east (Palmer 1896). Today, sport hunting, pest control and better farm management apparently prevent serious outbreaks of black-tailed jackrabbits. This species is expanding in range and conservation of the white-sided *L. callotis*, antelope and white-tailed jackrabbits may require some reduction in competition from this more adaptable hare.

White-sided Jackrabbit *Lepus callotis* Wagler 1830

Description

The white-sided jackrabbit is of medium size (2.7kg) with a relatively short hind foot (126mm) and enormous ears (138mm). According to Hall (1981) the upper pelage is dark, slightly pinkish buff, the rump grey, sides and underparts white and the ears lack black tips. The nape is brown to blackish and the upper part of the tail is black (Anderson and Gaunt 1962).

Distribution

North from Oaxaca, Mexico, along the Sierra Madre to Chihuahua and East Sonora. In the United States the white-sided jackrabbit is classified as endangered, being restricted to two valleys in Hidalgo Co., New Mexico, where the population has apparently declined by half between 1976 and 1981 because of habitat changes favoring the black-tailed jackrabbit *L. californicus* (Bednarz and Cook 1984). (See Fig. 4.2).

Habitat and Ecology

In New Mexico the white-sided jackrabbit is restricted to high grasslands of *Bouteloua*, *Muhlenbergia*, *Buchloe*, *Lycurus*, and *Sitanion*, at 1,500 to 1,600m. Surrounding areas have lower rainfall and higher evaporation, resulting in a grass-shrub complex which is occupied by the black-tailed jackrabbit (Bednarz 1977). Since 1976 these high grasslands have deteriorated, with an increase in shrubs. The corresponding increase in black-tailed jackrabbits at the expense of white-sided jackrabbits indicates the importance of open grassland habitat (Bednarz and Cook 1984).

The home ranges overlap, as in other hares, but there is no estimate of range area. White-sided jackrabbits will move at least a mile to feed or when disturbed (Bednarz and Cook 1977). The densities recorded in 1976 (1:34ha) were halved by 1981 (Bednarz 1984), and are far lower than the 1:1ha that black-tailed jackrabbits may reach. The food eaten is 99% grasses, including *Buchloe dactyloides*, *Bouteloua gracilis*, *Hilaria mutica*, *Panicum obtusum* and *Muhlenbergia torreyi* but in the dry season they may dig for roots of *Cyperus rotundus* (Bednarz 1977).

Behavior

Breeding behavior of the white-sided jackrabbit is similar to that of the black-tailed jackrabbits, except that there is a strong pair bond and the male will defend its mate. It is strictly nocturnal, apparently more so than the antelope *L. alleni* and

black-tailed jackrabbits. The white side fur is raised and flashed towards a pursuer and the hare may also leap high in the air and flash at the peak of its jump, landing where it started from. Three calls have been noted: the usual scream on being handled, harsh nasal grunts by a dominant male towards a subordinate, and a trilling grunt when the male is pursuing the female (Bednarz 1977).

Reproduction

The breeding season is unknown, but extends at least from mid-April to mid-August, allowing at least three litters a year. The average litter size from ten females in the literature is 2.2 (1-4) (Bednarz 1977).

Status and Summary

The white-sided jackrabbit appears to be a relatively rare species. Although little is known of its numbers in Mexico, it is likely that changes in habitat with overgrazing will favor the black-tailed jackrabbit. Information on the status of the white-sided jackrabbit in Mexico is urgently needed.

Cape Hare *Lepus capensis* Linnaeus 1758

Taxonomy

The Cape hare has a vast geographic range from South Africa to East China. There are 80 subspecies (including *tolai* and *granatensis*), but the whole group is in need of revision and many are likely to be invalid. Some, however, could turn out to be distinct species, and all could be of interest in evolutionary terms. *L. c. granatensis*, for example, could be a separate species restricted to Spain, and the taxonomic status of the hares of some Mediterranean Islands has still to be clarified.



Cape hare *Lepus capensis* in the Rift Valley, Kenya
(Photo by J.E.C. Flux)

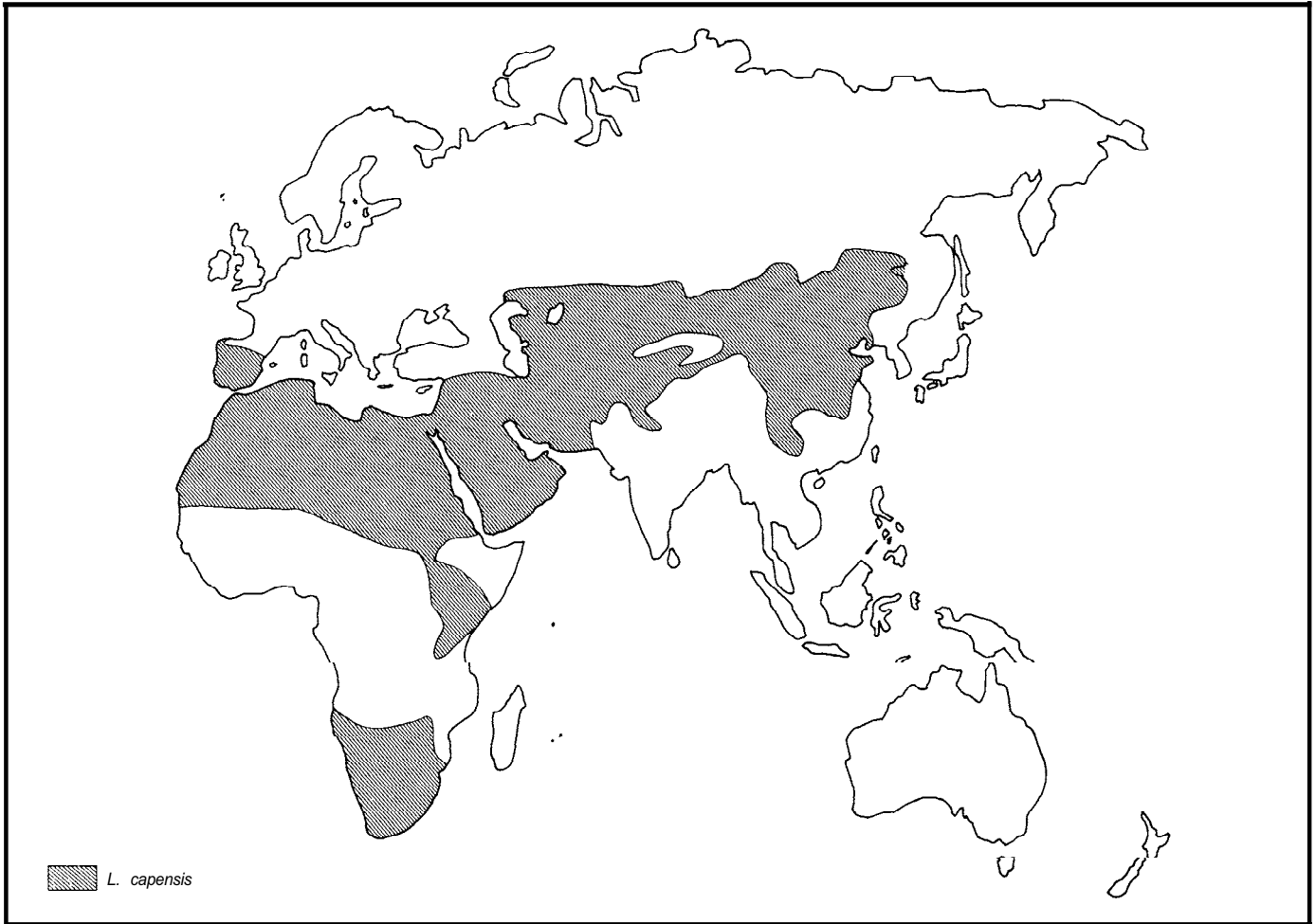


Figure 4.5 Distribution of the Cape hare *Lepus capensis* in Africa and Asia

Description

The subspecies vary greatly in size and appearance. Body weights range from about 1kg to 3.5kg, and coloring from very pale sandy buff to rich almost rusty brown on the back, white below. The ears in desert forms may be pale-edged; others have a narrow black edge at the top rather than a triangular patch as in the European hare *L. europaeus*, and the fur is very soft and straight.

Distribution

The Cape hare occurs over most of Northern, Southern and Eastern Africa, the Mediterranean, Israel, Arabia, Iran, Pakistan, north India, southern Russia and most of northern China, wherever there is suitable grassland, steppe or desert habitat, from sea level to 3,000m (Fig. 4.5). Like the black-tailed jackrabbit *L. californicus* it thrives on overgrazed pasture and is therefore expanding its range at the expense of less adaptable hares.

Habitat and Ecology

Practically any open country is suitable habitat for the Cape hare; from rich savanna grassland on the equator in Africa (Fig. 4.5) to cold stony desert in the Gobi in Mongolia, where they are most numerous in river valleys but also occur with marmots at 2,400m on alpine meadows (Ognev 1966). Pasture that has been overgrazed by domestic stock is favored, and in East Africa fires that remove scrub also extend the range of Cape hares (Flux and Flux 1983). In Arabia, according to Harrison (1972) "These most versatile, mobile and adaptable mammals are found in a wide variety of habitats . . . sand desert, steppe, scrubland, agricultural country or mountain terrain, in fact wherever there is sufficient vegetation, however sparse..."

Although Cape hares are game animals in some countries and used for meat and fur in others, their recent changes in distribution probably reflect human pastoralism and the felling of forest rather than intentional introductions. The result,

nevertheless, has been a most confusing mixing of gene pools which will not be clarified without great effort. Hence the status of many “subspecies” is totally unknown; some may be entirely separate species, others incipient species or former species now lost by hybridisation and some may be merely clines.

Home ranges of Cape hares have rarely been measured and will undoubtedly vary widely with habitats. Densities are higher in agricultural habitats and valleys than on mountain pasture and steppe (Ognev 1966). For the Orange Free State, Wessels (1978) estimated densities of 4.7-24.8 hares/km². In the Serengeti, Frame and Wagner (1981) estimated densities of 9.3 hares/km² on long-grass plains and 4.2/km² on short-grass plains, but some of the hares in the former habitat may have been *L. crawshayi* (= the African savanna hare *L. victoriae*); the overall density for the area was 8.5/km². For the same region, Curry-Lindahl (1981) estimated hare densities of 121/km², and for other parts of Africa, a range from 32/km² in semi-desert in Kenya to 167/km² in Kruger National Park. From our experience, however, Curry-Lindahl's estimates seem too high for East Africa (Eltringham and Flux 1971) and there is little evidence of any regular seasonal or annual cycle in numbers. In the same area, the Cape hare and African savanna hare ate *Digitaria* predominantly, with the Cape hare then taking more *Themeda triandra* and dicots than the latter (Stewart 1971). Diet in other habitats has been little studied and will undoubtedly vary widely.

Behavior

The behavior of Cape hares in East Africa is reviewed by Flux (1981b). They are strictly nocturnal, so much so in East Africa that eagles can very seldom catch them (L. Brown pers. comm. 1967). Where hares have not been shot at in the past, they stop at the sound of a gun and can sometimes be picked up by hand with a spotlight, as in Mexico (Griffith and Evans 1970). A major difference in behavior between the Cape hare and African savanna hare is that the former runs into the open when disturbed while the African savanna hare runs for cover - this behavioral difference is reflected in heart weight also (Flux and Flux 1983). Compared with the European hare, the Cape hare is more solitary, with only four groups of three in about 800 animals observed (Flux 1981b). In the Namib Desert, the Cape hare may make short burrows to shelter from the sun (Dixon 1975).

Reproduction

Near the equator breeding is continuous and the Cape hare produces eight litters a year, the litter size varying with the rainfall seasonally from 1.3 to 2.0 in different months (Flux 1981a). In central Russia the tolai hare (*L. capensis tolai*) has a six to seven month breeding season, with a litter size increasing seasonally from two up to four. Ognev (1966) quotes Luhashkin that the tolai hare in Manchuria has only two litters a year, but the litter size is not mentioned.

Status and Summary

Under present nomenclature, the Cape hare is probably the most abundant of all *Lepus* species. Despite this, their taxonomy is so uncertain that some subspecies may well be fully separate species. Some tiny forms such as *L. c. jeffreyi* on Masirah Island and *L. c. atallahi* on Bahrein are so distinctive that, regardless of taxonomic status, they merit conservation attention. An enormous amount of work remains to be done to solve this problem. As with the European hare in Europe, some populations of Cape hare in China have declined in the past ten years because of intensified agriculture and increased use of pesticides (Gao Yaoting, pers. comm. 1989).

Broom Hare

Lepus castroviejoi Palacios 1977

Description and Taxonomy

This species is of medium size averaging 2.7kg (2-3.2kg) with fur of a rich tawny brown similar in color and texture to the European hare *L. europaeus*, which it closely resembles. According to Palacios (1977) the broom hare is generally more brownish-yellow than the European hare *L. europaeus* or *L. granatensis* in Spain.

Genetic and distributional studies indicate that this species does not interbreed with adjacent populations of the European hare *L. europaeus* and *L. granatensis* (= *L. capensis*) (Palacios 1977, 1980). On the other hand, Schneider and Leipoldt (1983) found no difference in DNA patterns between broom and European hares and suggest they are conspecific.

The broom hare has a very small range and there are no subspecies.



Figure 4.6 Distribution of the broom hare *Lepus castroviejoi* in Spain

Distribution

Restricted to the Cantabrian Mountains (Northern Spain) between the Sierra de **Anceres** (to Lugo and Leon) and the Sierra de **Pena Labra** (to Santander and Palencia). This region is approximately 230km from east to west and 25-40km from north to south. (See Fig. 4.6).

Habitat and Ecology

The broom hare lives in mountains at 1,300-1,900m, descending in winter to 1,000m to avoid snow. The habitat is heath-land, mainly *Erica*, *Calluna*, and *Vaccinium*, with much shrub cover of *Cytisus*, *Genista*, and *Juniperus*. It also inhabits clearings in mixed deciduous forest of oak and beech (Palacios 1977).

Little is known about the home range, population density and food preferences, but they are likely to be similar to those of European hares in comparable habitat. Palacios and Ramos (1979) state that the broom hare is relatively abundant, but that hunting is excessive at the western edge of its distribution, where the hares are isolated from the rest of the population during the summer.

Behavior

The general behavior is likely to be similar to that of the European hare. Movement to lower ground in winter (Palacios and Meijide 1979) is unusual compared with the European hare in New Zealand (Flux 1967b).

Reproduction

No information available.

Status and Summary

The broom hare appears to be very recently evolved from the European hare, if not conspecific. Its main distinguishing features are skull characters which show remarkably little variation between individual animals. This suggests that the broom hare has perhaps expanded recently from a small founding population. The recommendations of Palacios and Ramos to restrict hunting in the west of its distribution should be supported.

Yunnan Hare *Lepus comus* Allan 1927

Subspecies: *Lepus comus comus*, *Lepus comus peni*, *Lepus comus pygmaeus*

Description and Taxonomy

The Yunnan hare is a small species (weight 2.0kg, 1.5-2.5), possibly related to the woolly hare *L. oiostolus* and included in that species by many taxonomists, although it may well be a northern form of the Indian hare *L. nigricollis*. Its color is greyish brown above, with bright ochraceous mixed with yellow on the sides, a grey rump, and the tail is dark on the upper surface (Wang *et al.* 1985).

There are three subspecies: *L. c. comus* in West Yunnan:

L. c. peni from central Yunnan east to Guiyang City, from Bijie and Muli in the north to Luodian and Huidong in the south; and *L. c. pygmaeus* from the north near the Yangtze River to central Yunnan.

Distribution

This is a mountain species living throughout Yunnan, except that part southwest of the Mekong River, and in the western half of Guizhou. (See Fig. 4.4).

Habitat and Ecology

Very little is known about the Yunnan hare, which presumably occupies the high montane pastures in equivalent habitat to the woolly hare in Tibet. Its specific difference from the woolly hare is based on its small size, the small, flat and low supraorbital process and the proportions of the diastema and toothrow. The brighter fur coloring is also considered diagnostic (Wang, Luo and Feng 1985; Luo 1988), although Gao Yaoting (pers. comm. 1989) points out that the grey rump is a character of the woolly hare.

Behaviour and Reproduction

Nothing recorded.

Status and Summary

The remote habitat of this species is unlikely to be threatened, but increasing agricultural development in the valleys may isolate mountain populations. More work is needed on behaviour, habitat, and taxonomic relation to the woolly hare and Indian hare.

Korean Hare *Lepus coreanus* Thomas 1892

Taxonomy and Description

The Korean hare is a medium-sized species a little larger than the Chinese hare *L. sinensis*. The fur is considerably heavier, and more blackish in color on the back. It is of uncertain taxonomic position. Corbet (1978) says "there is no doubt of its close relationship with *L. sinensis*", while Kim and Kim (1974) consider it the same as the Japanese hare *L. brachyurus*. We suggest it is closest to the Manchurian hare *L. mandshuricus*, but here follow Jones and Johnson (1965) in according it specific status.

Distribution

Widely distributed in lowland Korea, Southern Manchuria (Won 1961) and some mountainous areas and may extend into mainland China (Kim and Kim 1974). They are also present on three of the five largest offshore islands. (See Fig. 4.7).

Habitat and Ecology

The Korean hare is very common on the plains (rather than the hills) and villagers trap them for food. It is a well-known game animal (Won 1961), but is also a pest in forestry planta-

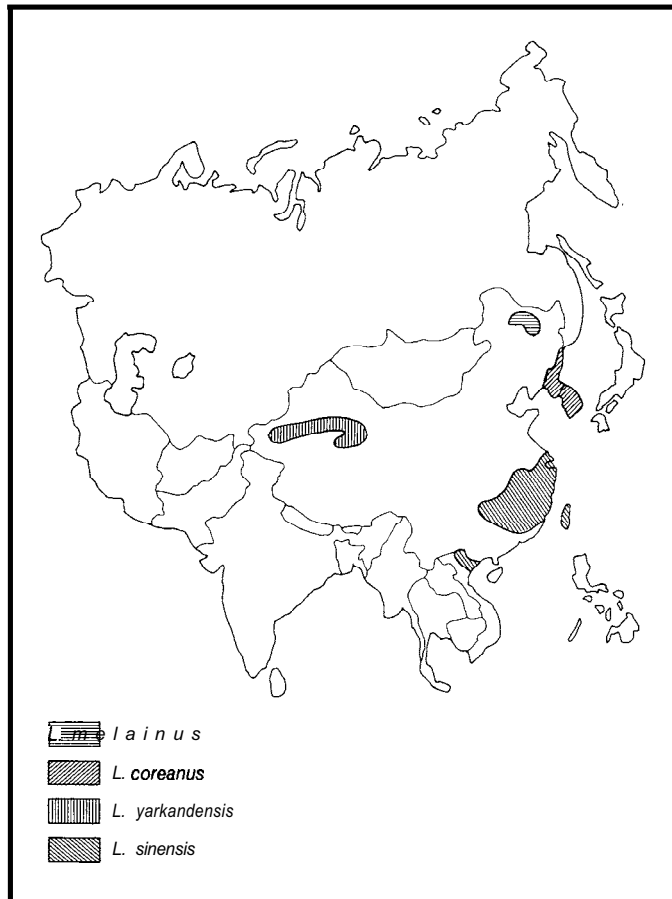


Figure 4.7 Distribution map of the Korean hare *Lepus coreanus*, Manchurian black hare *L. melainus*, Chinese hare *L. sinensis* and Yarkand hare *L. yarkandensis*

tions (Kim and Kim 1974). According to Howard et al. (1975), hares are a problem to barley growing near the mountains in Kyeonsnam Province and in Jeonnan Province they girdled half the peach trees growing on a five hectare farm.

The population density increased from 2.7/km² in 1969 to 4.8/km² in 1973, averaged over eight provinces, with peak density of 18.3/km² (Kim and Kim 1974). In different habitats, densities range from 5.1/km² in the mountains and 4.1/km² on hills to none on cultivated land or by the coast. In the best habitat, forest on Mt. Toham, a density of OS/ha was recorded (Kim and Kim 1974).

Behavior

Apart from damage to agriculture and forestry, little has been recorded. Won (1961) states that 200 adults were captured in one drive at Kwangnung, but it is unlikely that the hares are gregarious. This author shot one in a pine forest, and records that a villager captured another on Mt. Solak at 500m.

Reproduction

No information available.

Status and Summary

This species seems reasonably common, but its taxonomic status and relationship with the Chinese hare and Manchurian hare require investigation.

European or Brown Hare *Lepus europaeus* Pallas 1778

Subspecies: *Lepus europaeus alba*, *Lepus europaeus argenteogrisea*, *Lepus europaeus biarmicus*, *Lepus europaeus borealis*, *Lepus europaeus caspicus*, *Lepus europaeus caucasicus*, *Lepus europaeus cyrensis*, *Lepus europaeus europaeus*, *Lepus europaeus flavus*, *Lepus europaeus gallaecius*, *Lepus europaeus hispanicus*, *Lepus europaeus hybridus*, *Lepus europaeus hyemalis*, *Lepus europaeus granatensis*, *Lepus europaeus iturissius*, *Lepus europaeus kalmykorum*, *Lepus europaeus karpatorum*, *Lepus europaeus medius*, *Lepus europaeus meridiei*, *Lepus europaeus meridionalis*, *Lepus europaeus niethammeri*, *Lepus europaeus niger*, *Lepus europaeus occidentalis*, *Lepus europaeus pamassius*, *Lepus europaeus ponticus*, *Lepus europaeus pyrenaicus*, *Lepus europaeus tesquorum*, *Lepus europaeus transsylvanicus*, *Lepus europaeus tumak*

Taxonomy

The 30 subspecies given above are of very variable status.

Description

The European hare is a large animal, averaging 3.8kg (3-5kg) in weight, of relatively uniform appearance. The fur is long and curled on the back, with a tawny or rusty color over the chest and sides, darker above, white below; and the tail is large and conspicuous, black on top and white underneath. The tips of the ears have a large triangular black patch on the back contrasting with the paler grey of the rest of the ear. In winter there is some white on the sides of the head and base of the ears, and grey on the haunches.

Distribution

Over most of Europe to 60°N, except for Ireland, the Mediterranean region and Scandinavia, which all now have introduced populations. To the east, European hares have expanded in range naturally and by liberations to Siberia and the south Pacific coast of Russia; in the south they are replaced by the tolai hare *L. capensis tolai* and to the north by the mountain hare *L. timidus*. Because they are important game animals, populations have been introduced successfully in eastern Canada, northeastern United States, most of South America between 28° and 45°S, Australia and New Zealand. Small introduced populations occur on several North Sea islands, Barbados, Reunion and the Falkland Islands. (See Fig. 4.8).

Habitat and Ecology

Open country with scattered shrubs or hedges for cover is good habitat for European hares. They are very adaptable and

reach high densities on mixed farmland under intensive agriculture in Denmark, Germany and Poland. Modern techniques, with large fields for mechanized agriculture and the excessive use of herbicides and pesticides, has led to recent population declines in Britain and Europe (Schneider 1978, Tapper and Barnes 1986). Other suitable habitats range from moorland, saltmarsh, alpine grassland, deciduous and evergreen open woodland, steppe and near desert. Where no other *Lepus* are present, as in Chile, Argentina, Australia and New Zealand, the habitats occupied can be especially variable, including pampas, sand dunes, marshes and alpine fell-field.

The food eaten varies with the habitat: in Europe hares on agricultural land eat 90% of soft greens, 5.5% woody plants, 2.2% root crops, 1.7% grain crops and 0.5% forest plants (Zörner 1977). In New Zealand alpine areas, hares ate short grass in summer, shrubs and tussock in winter (Flux 1967b). In hunting regions of Germany and Scandinavia they are fed hay in winter. Detailed lists of species eaten are given by Brull (1976) and Homolka (1987).

Estimates of home range vary from 38ha (16-78) in England (Tapper and Barnes 1986) to 53ha in New Zealand (Parkes 1984) and 330ha in Poland (Pielowski 1972). Population density in the Netherlands averaged 0.25/ha with peaks on an airfield of 2.4/ha (Broekhuizen 1976). In Poland the best 20% of hunting areas had 0.5/ha, the rest 0.1-0.3/ha (Pielowski 1976). The highest record is 3.4/ha for a 100ha island off Denmark (Abildgard, Andersen and Barndorff-Nielsen 1972).

Behavior

The European hare is largely nocturnal, but may start feeding in mid afternoon in higher latitudes and in the breeding season. They may move up to 1.8km to reach grazing in Scotland (Hewson and Taylor 1968) and can travel 15km while feeding in one night (Flux 1967b). Feeding takes about a third of a hare's time, and before entering its "form" for the day it backtracks to confuse predators (Flux 1981b).

Reproductive behavior reaches a peak in spring (Mad March hares) with up to a dozen males congregating round a female in oestrus, boxing each other and chasing off rivals (Schneider 1978). A dominance hierarchy between individuals has been demonstrated at food (Lindlof 1978; Monaghan and Metcalfe 1985). Over much of their range European hares occur in the same habitat as rabbits *Oryctolagus cuniculus* and it is rather surprising that the far smaller rabbit dominates the hare (Flux 1981b).

Reproduction

European hares start breeding about the winter solstice in all nine countries where they have been studied except Argentina (Flux 1965; Amaya, Alsina, and Brandani 1979). In captivity superfoetation (fertilization of a female already pregnant that leads to her carrying embryos of different ages) is common, giving a mean interval between births of 38 days instead of the normal 42-day gestation period (Martinet 1977). Only three of 24 females with full-term embryos showed superfoetation in the wild (Flux 1967a). The mean litter size increases seasonally to a peak and then declines; there are normally three to

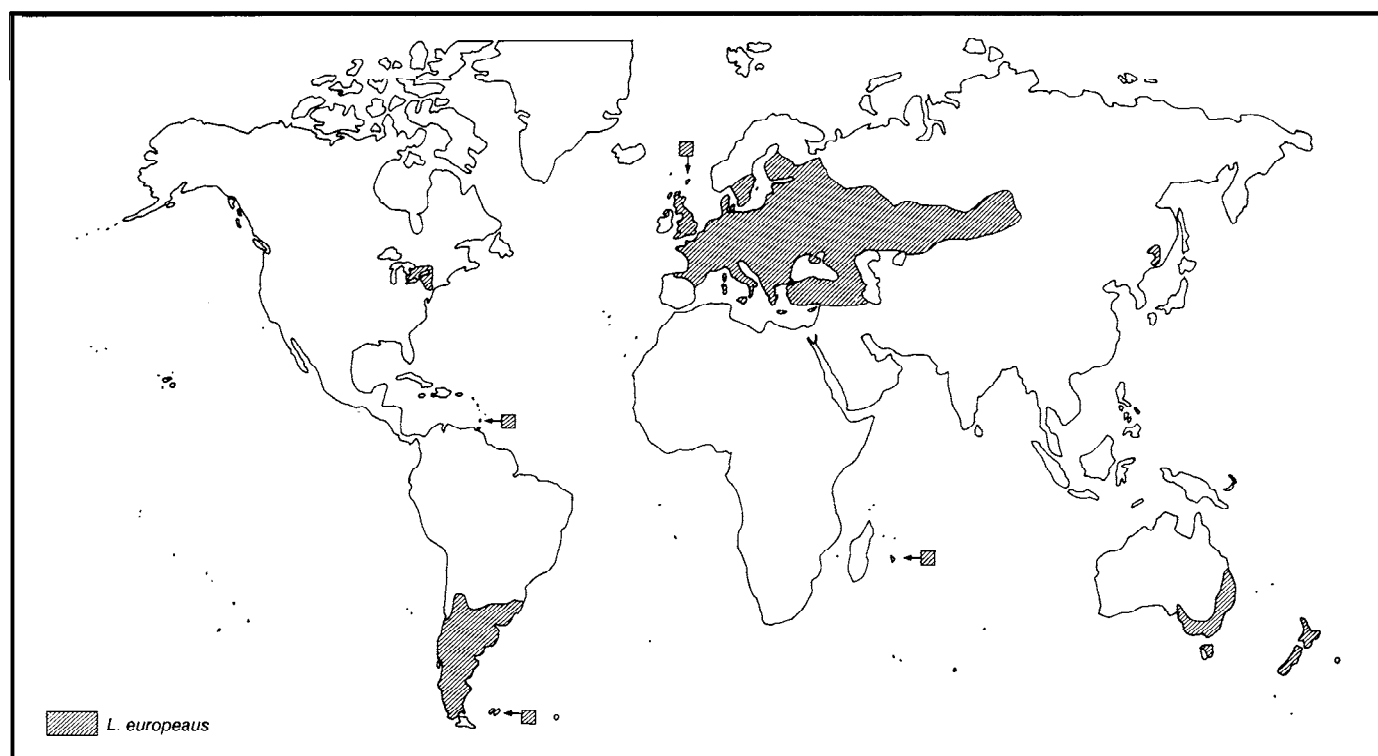


Figure 4.8 Distribution of the European hare *Lepus europaeus* worldwide



European hare *Lepus europaeus* in form at St Amaud, New Zealand
(Photo by J.E.C. Flux)

five litters a year. The annual production of young per female varies between 4.6 in Argentina and 13 in Czechoslovakia (Pepin 1989), but most populations are remarkably constant at around ten (Flux 1981a).

At birth leverets weigh 123g (100-165g) and grow at 19g (16-27g) per day until three months old. Nursing takes place once or twice a day, in the late evening, and lasts only a few minutes (Broekhuizen and Maaskamp 1980). Adult size is reached in five months and some early-born leverets may breed in their year of birth.

Status and Summary

The European or brown hare is probably the most important game animal in Europe, with over five million being shot each year. There is considerable concern over recent declines in Europe, but the populations are not really threatened. More serious from a conservation view is the total loss of regional forms, like the French and Danish ones, by massive importations from Hungary and Eastern Europe. The status of many

local populations and subspecies requires investigation and it was only recently that what is thought to be a new species was discovered in Spain (Palacios 1977). More taxonomic studies are urgently needed.

Ethiopian Hare *Lepus fagani* Thomas 1902

Description and Taxonomy

The Ethiopian hare is of medium size with long, dense, harsh fur. The color of the upperparts is buff ochraceous brown, the sides, nape and chest tawny. The tail is white or buff below, with a large blackish dorsal stripe above. Below the chin is greyish and the belly white. This species is closely related to the *L. victoriae*/*L. saxatilis* complex and is usually considered part of it. Azzaroli-Puccetti (1987), however, on the basis of more material, has separated it again because of its uniform character throughout its range.

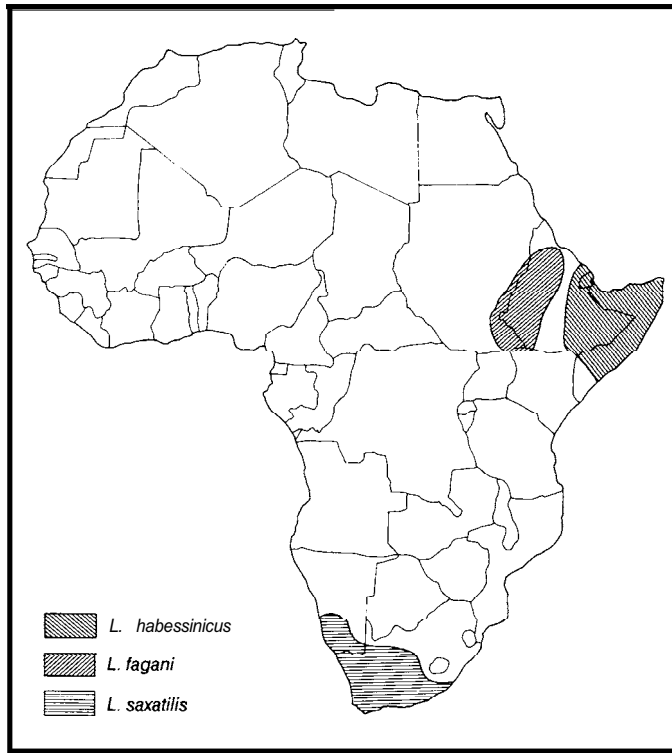


Figure 4.9 Distribution of the Ethiopian hare *Lepus fagani*, Abyssinian hare *L. habessinicus* and scrub hare *L. saxatilis* in Africa

Distribution

North and west Ethiopia on the plateau, and Kenya, at high altitudes. The type is from Lake Tana, Ethiopia. (See Fig. 4.9).

Habitat, Ecology, Behavior and Reproduction

Nothing recorded.

Status and Summary

The Ethiopian hare is probably a subspecies of the African savanna hare *L. victoriae* (or scrub hare *L. saxatilis*) but the mountain populations are geographically isolated, and the hares are probably also isolated by surrounding populations of Cape hares *L. capensis*. This isolation could have resulted in speciation and merits further research.

Tehuantepec Jackrabbit *Lepus flavigularis* Wagner 1844

Taxonomy and Description

The Tehuantepec jackrabbit is a large animal with long ears and looks like the white-sided *L. callotis* and antelope *L. alleni* jackrabbits. The upper parts are bright ochraceous buff strongly washed with black, the flanks, chin and underparts are white. The haunch and legs are very pale grey. The ears are uniform buff, with pale whitish tips, and the nape has a black stripe extending back from the base of each ear. Anderson and Gaunt (1962) regarded it as a distinct species related to the white-sided jackrabbit *L. callotis* but separated geo-

graphically from all other *Lepus* species. The black color on the nape that they considered a specific character is, however, known to be variable in the Indian hare *L. nigricollis*, its Old World counterpart. A numerical taxonomic analysis by Dixon *et al.* (1983) supported the retention of the Tehuantepec jackrabbit as a separate species.

Distribution

According to Chapman *et al.* (1983), the distribution of the Tehuantepec jackrabbit has been exaggerated and it exists only from Salina Cruz, Oaxaca, to the extreme west of the State of Chiapas, Mexico. The area occupied in the past was apparently 150km² but increasing clearance for agriculture is destroying most of its habitat. (See Fig. 4.1).

Habitat and Ecology

At present this jackrabbit is restricted to riparian vegetation, sand dune and shrub forest, which never exceeds a 4-5km wide strip along the shores of salt water lagoons on the north side of the Gulf of Tehuantepec. It co-exists with the eastern cottontail *Sylvilagus floridanus* and is exclusively nocturnal.

Behavior and Reproduction

Very little has been recorded. Two adult females collected on 7 February 1981 were pregnant, one with two embryos fully developed with CR lengths of 175 and 178mm (Dr. F.A. Cervantes, pers. comm. 1989).

Status and Summary

The Tehuantepec jackrabbit is recommended for listing as endangered because its habitat is threatened by encroaching agriculture as the local human population is expanding. In addition, the species is shot by numerous parties of hunters coming from cities up to 200km away to shoot deer by spotlighting at night. "We ask hunters, people of the areas, and they say there are still a few left, but when asked specifically, they don't know where" (Lopez-Forment 1989). This is clearly the most endangered *Lepus* species at present and requires urgent attention.



Tehuantepec jackrabbit *Lepus flavigularis*
(Photo by G. Ceballos)

Abyssinian Hare
***Lepus habessinicus* Hemprich and Ehrenberg 1832**

Taxonomy and Description

The Abyssinian hare is a small hare (weight about 2kg), with upperparts of a cineraceous color marked with black or grizzled black and buff. The tail is white below, black above, and the ears of moderate length with only a narrow black edging. About half the skulls have a separate interparietal bone, which is normally fused in *Lepus*, but also occurs commonly in Cape hares *L. capensis* (Angermann 1983). There is now some taxonomic consensus over the status of this hare, which Angermann (1983) considers a subspecies of the Cape hare *L. capensis*. Azzaroli-Puccetti (1987) agrees, "Probably . . . *L. habessinicus* warrants only subspecific status . . .", but also points out that the interparietal bone is usually absent in the Berbera population in northern Somalia, and retains specific rank pending future biochemical analyses.

Distribution

The Abyssinian hare is restricted to East Africa, especially Somalia, the eastern part of Ethiopia, and possibly Northern Kenya. (See Fig. 4.9).

Habitat and Ecology

This hare apparently replaces the Cape hare in the open grassland, steppe, savanna and desert habitats in the area occupied. Some scattered scrub is needed for shade by day and cover from predators, but thicker scrub is taken over by other hares in the *L. victoriae/L. saxatilis/L. fagani* complex.

Behavior and Reproduction

Nothing reported, but it is undoubtedly a nocturnal species very like the Cape hare.

Status and Summary

In our view, this hare is a subspecies of the Cape hare and is widely distributed and abundant. Like the Cape hare, it is probably spreading with the overgrazing of pasture by domestic stock.

Hainan Hare
***Lepus hainanus* Swinhoe 1870**

Description and Taxonomy

The Hainan hare is small (weight 1.5kg, 1.30-1.75) to judge from seven specimens weighed by Luo (1988). It has a smaller, more rounded head than the Chinese hare *L. sinensis* and brighter coloring. The back is tawny brown mixed with black, the sides chestnut brown, the top of the tail blackish with white below, the feet pale brown with white marks and the underparts white.

Taxonomically, the position of the Hainan hare is still uncertain. Most authors consider it a subspecies of the Burmese hare *L. peguensis*, which in turn is sometimes referred to as the Indian hare *L. nigricollis*. Swinhoe's original description of

"soft, woolly fur more like that of *L. timidus*" and "anterior upper incisors without the deep groove", however, are supported by recent descriptions and are not characters of the Indian hare. Specific separation may be simplest pending a full review of Southeast Asia hares.

Distribution

Restricted to Hainan Island, south China. (See Fig. 4.4).

Habitat, Ecology, Behavior and Reproduction

The greatest density of hares is in the dry grassland in the northwest and southwest of Hainan; the east of the island is less suitable. Flat, dry farm land with scattered second growth scrub or plantains is best, and hares do not live in the mountains or on agricultural land (Luo 1988, Song Yanling, pers. comm. 1989).

Behavior

The Hainan hare is nocturnal, with most activity after dark and in the early morning, although some may feed by day. They live among grass and do not dig burrows (Luo 1988).

Reproduction

Little recorded, but the young are said to survive well in dry weather.

Status and Summary

In previous years many hares were caught and the skins sold; some are still snared for the local market. Overhunting and agricultural development have reduced numbers to extremely low levels. Luo (1988) recommended protection to let numbers recover, when they could again be managed as a resource for hunting. A survey to assess the present numbers and implement conservation management is urgent, although it is unlikely that protection could be enforced without considerable public education (Song Yanling, pers. comm. 1989).

Black Jackrabbit
***Lepus insularis* Bryant 1891**

Description and Taxonomy

The black jackrabbit is of moderate size, about 2.5kg in weight. It is glossy black on the upper parts, but grizzled on the sides of the body, sometimes on the head, with dark buff or reddish brown. The underparts are dark cinnamon buff or dusky brown and the ears and sides of the head dusky grey.

This species is closely related to the black-tailed jackrabbit *L. californicus*, but the jugal bone is heavier and there are sufficient differences in the skull to separate the black jackrabbit from both *L. californicus* on the adjacent mainland and from other subspecies (*L. c. xanti*, *L. c. magdalenae*) on nearby islands (Dixon *et al.* 1983).

Distribution

The black jackrabbit is found only on Espiritu Santo Island in the Gulf of California. (See Fig. 4.2).

Habitat, Ecology, Behavior and Reproduction

No information available.

Status and Summary

Although this is a species with a very restricted distribution, Chapman et al. (1983) consider that "As it is unlikely that the island will ever be inhabited the hares seem in no danger and the population is stable". To ensure this, however, it may be wise to obtain more information on habitat requirements and consider establishing another population on some nearby island.

Manchurian Hare

Lepus mandshuricus Radde 1861

Description and Taxonomy

This is the smallest of the four species of hares in Manchuria, weighing 1.8kg (1.4-2.6kg). The fur is soft, long and thick. The back is blackish brown or rust brown with light yellow banded hairs, the breast, flanks and legs pinkish cinnamon, ears cinnamon buff, the neck dull rust-brown, belly whitish and tail grey with blackish-brown on top. In winter the fur is paler, some individuals have an ash-grey tinge, and the underparts are white.

The Manchurian hare has had a varied taxonomic career, having been shifted to the genus *Caprolagus*, then *Allolagus*, and finally back to *Lepus* again. It seems most closely related to *L. brachyurus* of Japan, but merits specific distinction (Angermann 1966).

Distribution

In the north, this hare reaches the Bureya Mountains (c. 50°N), is widely distributed in northern Manchuria, and may extend into Korea (Jones and Johnson 1965). It is a forest species, and after the forests are cleared the tolai hare *L. capensis tolai* takes over the area (Loukashkin 1943) as it now has in eastern Manchuria. (See Fig. 4.4).

Habitat and Ecology

The preferred habitat is mixed forest, not pure conifer, on ridges and southern slopes, especially where tall Mongolian oak with an undergrowth of Manchurian hazelnut is dominant (Loukashkin 1943, Ognev 1966) and creepers and vines make the forest impenetrable. Hilly country is favored, with cliffs and rock outcrops, from 300m to 900m altitude. The Manchurian hare does not like open valleys or grassland, and never approaches human habitation. Little is known of the ecology of this species, but it seems to be the Old World ecological equivalent of the snowshoe hare in North America, feeding on twigs of willow, linden, maple, wild apple, birch, elm, various shrubs and herbs and fallen fruit (Angermann 1966).

Behavior

The Manchurian hare is presumably solitary, but "wide beaten tracks" are produced in favored habitat in thick for-

ests. It is "very shy" and does not have lairs in the open like most hares, settling "in holes in tree trunks which are open on one side" (Radde 1862, quoted by Ognev 1966).

Reproduction

Breeding begins in mid-February, and the litter size is one or two, occasionally four to five. The number of litters per year is not recorded (Angermann 1966).

Status and Summary

The Manchurian hare is restricted to a forest habitat which is declining rapidly in area. Because the land is then occupied by the tolai hare *L. capensis tolai* any subsequent regrowth of forest may not be accessible and plantation forestry is likely to be too lacking in understorey plants. Investigation of natural forest parks and reserves for hare populations is required.

Manchurian Black Hare

Lepus melainus Li and Luo 1979

Description and Taxonomy

According to Ognev (1966), Sowerby (1923) confirmed that the Manchurian black hare was smaller than the Manchurian hare, although this is not supported by the weight of five black hares given by Luo (1988): 1.84kg (1.7-2.05). The back and flanks are shiny black with a slight brown tinge, the throat and chest cinnamon-buff, the belly white, the ears are black with a rusty fringe and the tail dark grey with black on the top. Some very long pale straw-colored hairs contrast with the dark back and flanks. There is a small white spot on the head. Previous authors have considered the black hare a dark form of the Manchurian hare *L. mandshuricus* because the dark form seems to be rather variable, it is not geographically isolated and the density is low (Gao Yaoting, pers. comm. 1989). A few pure black hares also occur in Manchuria; whether these are melanics of *L. mandshuricus* or *L. melainus* is unclear (Ognev 1966).

Distribution

Rare in the Ussuri Territory, but as common as the Manchurian hare farther south in the Kirin Province (Ognev 1966). (See Fig. 4.7).

Habitat and Ecology

Presumably the same as the Manchurian hare. The Manchurian black hare may be adapted to dark forest or concealment in burrows or hollow trees.

Behavior and Reproduction

No information available.

Status and Summary

The taxonomic status of this species requires verification by biochemical methods and investigation of its life history and ecology. The widespread success of a melanic form which is

not isolated on an island is unusual. The species would apparently be vulnerable to loss of forest and, as for the Manchurian hare *L. mandshuricus*, its status in reserves should be established.

Indian Hare *Lepus nigricollis* F. Cuvier 1823

Subspecies: *Lepus nigricollis a yabertensis*, *Lepus nigricollis cutchensis*, *Lepus nigricollis dayanus*, *Lepus nigricollis joongshaiensis*, *Lepus nigricollis macrotus*, *Lepus nigricollis rajput*, *Lepus nigricollis ruficaudatus*, *Lepus nigricollis mahadeva*, *Lepus nigricollis sadiya*, *Lepus nigricollis singhala*, *Lepus nigricollis simcoxi*, *Lepus nigricollis tyleri*

Description and Taxonomy

The Indian hare is of moderate size, averaging 2.5kg (1.8-3.6kg), and tends to be larger towards the south of India. The fur is rufous-brown much mixed with black on the back and face, rufous on the breast and legs, and the chin and underparts are white. The southern form (*L. n. nigricollis*) has a dark brown or black patch on the back of the neck and a black

upper surface to the tail; in the north (*L. n. ruficaudatus*) these parts are grey and brown, respectively. The desert form (*L. n. dayanus*) has paler, yellow-sandy coloration and females (2.2kg) are on average heavier than males (1.8kg), according to Prakash and Taneja (1969).

There are 12 subspecies, but several of these might be full species or even belong to the Cape hare *L. capensis*. A revision of Indian hares is overdue.

Distribution

Indian hares range from the foot of the Himalayas to the extreme south of India, from Pakistan to Assam and Bangladesh except in the Sunderbunds. They also occupy Sri Lanka. In Java they are restricted to the extreme west of the island and may have been introduced. Other introduced populations are on Mauritius and the nearby island of Gunners Quoin, Analega, Reunion, and Cousin island in the Seychelles. (See Fig. 4.10).

Habitat and Ecology

This species occupies a wide range of habitats, from open desert with scattered shrubs near Jodhpur to thick jungle, provided there are some open clearings. Large tracts of scrub

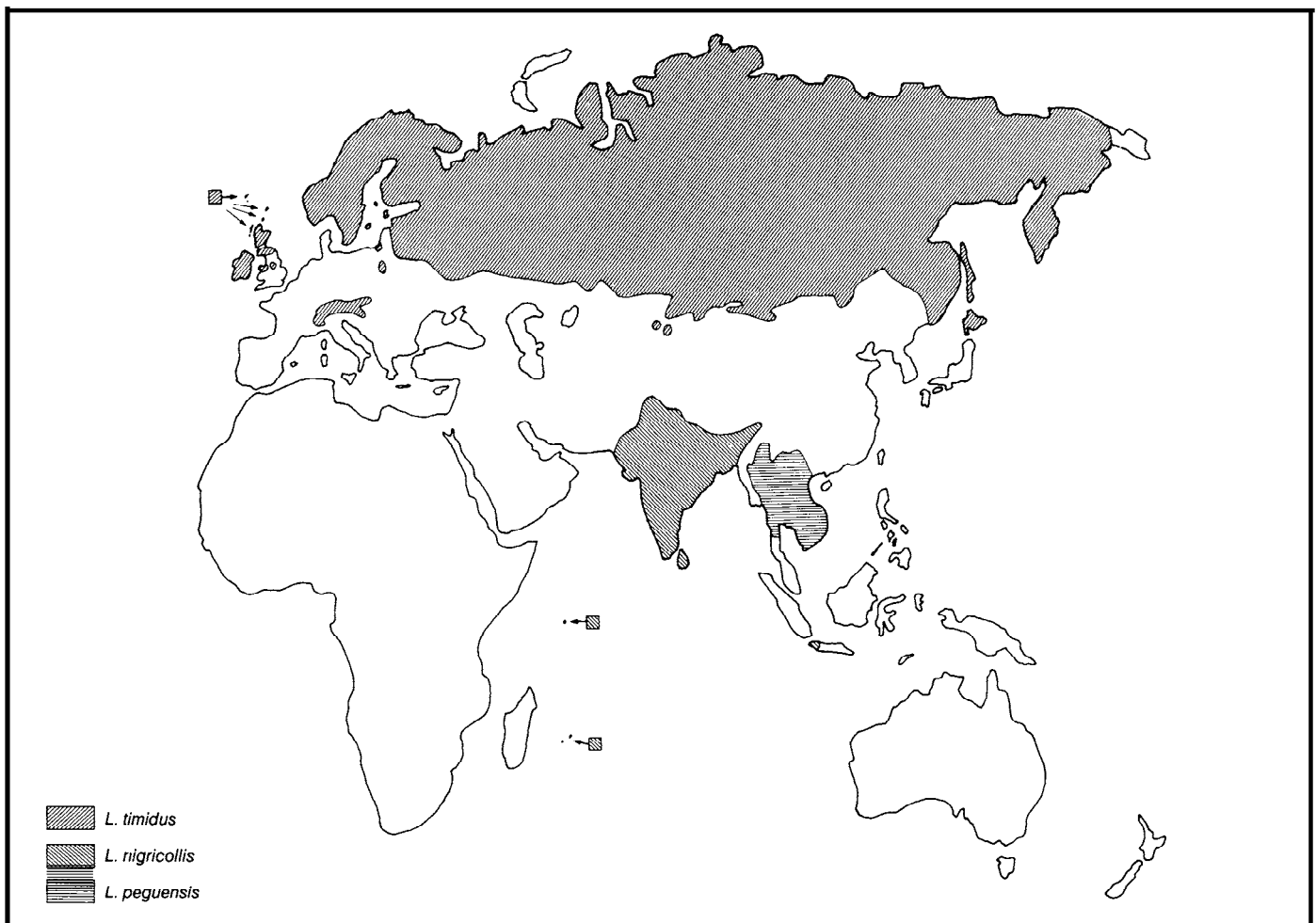


Figure 4.10 Distribution of the Indian hare *Lepus nigricollis*, Burmese hare *L. peguensis* and mountain hare *L. timidus* in Eurasia



Indian hare *Lepus nigricollis* (Photo by W. L. R Oliver)

and wasteland alternating with cultivated plains are ideal habitat (Prater 1971). In the Nilgiri Hills they live over 2,000m, and in the Himalayas up to 2,400m, where they apparently give way to the Cape hare *L. capensis* or woolly hare *L. oiostolus*.

The main diet is grass and forbs. In the Sind Desert they spend the day under bushes and come out at night to feed on *Capparis*, *Panicum*, *Crotalaria* and *Zizyphus* (Purohit 1967). In wetter regions the diet contains up to 73% grasses and in the dry season hares may travel 100-500m to reach green vegetation (Sabnis 1981). Grass, young plants, sweet potato and lettuce from gardens are recorded as eaten in Sri Lanka (Phillips 1935). On Cousin Island a detailed analysis of cuticle fragments in hare droppings listed sedges and grasses as major constituents, with *Achyranthes aspera* and *Ficus reflexa* in another area (Kirk 1981). Indian hares may damage young trees and agricultural crops (Prakash and Taneja 1969), peas (Ghose 1971) and groundnuts in Pakistan (Brooks *et al.* 1987). In western Nepal, hares spent the day in short grassland-shrub forest areas and foraged at night on short grass and crops (Bell 1986).

Home ranges have been measured in Nepal (1-10ha, Bell 1986) and on Cousin Island (0.7-1.6ha, Kirk 1981), but larger ranges are likely in more open country and desert. Population density was estimated at 0.25 hares/ha in Nepal (Bell 1986) and 5.8/ha on Cousin Island; the latter is a good example of the unusually high densities hares can reach on isolated islands without predators.

Behavior

Indian hares are normally nocturnal unless disturbed and often seen in the headlights of vehicles at night (Krishnan 1972). During the day a series of forms may be used for shelter, in low shrubs, tall grass, *Zizyphus*, or young palms; a

single animal may use different dens in the morning and afternoon depending on the weather, sometimes returning to a form after disturbance (Ghose 1971). When pursued, they may take to ditches or animal burrows for cover. Hares living at high density on Cousin Island became active in mid afternoon, usually feeding in the shade of trees (Kirk 1981).

Reproduction

In a detailed study near Jodhpur, Prakesh and Taneja (1969) found fertile male hares every month; some females were pregnant in all months, but peak breeding and litter size were during the monsoon. The average annual litter size was 1.8 (1-4), rising from one in the winter to 3.2 in July.

Status and Summary

Indian hares are shot as game and snared or netted by villagers to prevent crop damage. Many were formerly killed by predators; however, these are declining in India as human populations increase, so on balance the environment is probably improving for hares. Ghose (1971) points out that many hares live close to human habitation.

A major problem is the uncertain taxonomic status of hares included under the name *L. nigricollis*. For example *L. ruficaudatus* could well be a distinct species. McNeely (1981) suggested that the Javan hare was probably an endemic species in view of its long fossil history there. If so, it would merit urgent action because its numbers are now very low (Dr. Boead, pers. comm. 1989).

Woolly Hare *Lepus oiostolus* Hodgson 1840

Subspecies: *Lepus oiostolus grahami*, *Lepus oiostolus kozlovi*, *Lepus oiostolus oiostolus*, *Lepus oiostolus przewalskii*, *Lepus oiostolus qinghaiensis*, *Lepus oiostolus qusongensis*, *Lepus oiostolus sechuenensis*.

Description and taxonomy

The woolly hare, as its name suggests, has long curly hair, the color varying widely between different subspecies from dark greyish-brown (*L. o. grahami*) to pale sandy yellow (*L. o. oiostolus*). The rump is paler and greyer than the back and the tail varies from pure white to dirty white below, with a broad brown stripe above. It is a moderate to large species, weighing 2.5-3kg in the north of its range, 2-2.5kg in the south, with some individuals reaching 3.75kg (Cai and Feng 1982).

The taxonomy is still somewhat confused. Kao and Feng (1964) listed five subspecies and included the Yunnan hare *L. comus*. More recently Cai and Feng (1982) separated *L. comus* and listed the subspecies given above.

Distribution

The woolly hare occurs on mountains from 2,500m to 5,400m in Tibet, Gansu, Szechuan, Sikkim, Nepal and Kashmir (Angermann 1967b). *L. o. oiostolus* occupies the western half

of the range, from 79°E to 92°E, and the other subspecies from 92°E to 103°E, in latitudes 27°-37°N. (See Fig. 4.4).

Habitat, Ecology, Behaviour and Reproduction

This species inhabits high alpine meadows and mountain slopes up to the snowline; also dry, arid plains covered in stones. It takes cover in marmot burrows and shelters among rocks. There is very little detailed information about the woolly hare, but numbers seem to be very low except in a few favoured areas. Thus Shaller *et al.* (1988) write of Qinghai and Gansu Provinces: "Woolly hares *Lepus oiostolus* were generally scarce. However, parts of the Shule Nanshan block had a hare eruption - 17 animals were counted in one 250m stretch."

Status and Summary

More field work is needed on this species. Angermann (1967b) considers that it probably moults only once a year, in which case it cannot change colour in winter and would be very conspicuous against the snow unless it migrates downhill. If it needs forest for cover in winter it may be adversely affected by the decline in this habitat over much of its range, but there seems to have been relatively little change to its open grassland habitat. It may also have been poisoned accidentally in pika control operations.

Alaskan Hare *Lepus othus* Merriam 1900

Description and Taxonomy

The Alaskan hare is one of the largest hares, averaging 4.8kg (3.2-6.5) for a sample of 83 animals (Anderson and Lent 1977). In summer the coat is brown (cinnamon drab) above, white below; in late September the winter moult begins and the coat becomes completely white except for black tips on the ears. The spring moult starts in late May (Howell 1936).

Hall (1981) recognized two subspecies: *L. o. othus* in the west and *L. o. poadromus* in southwest Alaska, but Anderson (1974) regards these as extremes in a continuous cline. The species is now normally regarded as conspecific with the arctic hare *L. arcticus* (Baker *et al.* 1983) and sometimes both are included in the mountain hare *L. timidus* (Dixon *et al.* 1983).

Distribution

West and southwest Alaska, from sea level to over 2,000ft (600m). Their former distribution may have extended north-west to Barrow, as shown on the maps of Howell (1936) and Hall (1981), but the present distribution does not apparently include the arctic slope (Anderson 1978). (See Fig. 4.3).

Habitat and Ecology

Open tundra is the normal habitat, with rocks for cover on alluvial plain for the northern subspecies, while the southern population occupies coastal lowland areas on the Aleutian Island chain. There appear to be no studies of home range or density and the animal is usually described as rare. The food is

likely to be the same as that taken by other arctic hares: dwarf willow, grasses, sedges and heath plants. Anderson (1974) records *Salix alaxensis* and *Empetrum nigrum* eaten in April and May.

Behavior

Apart from Walkinshaw's (1947) description of a pet hare, there seems to be little recorded. The lack of records of colonial behavior is surprising; either this species differs from other arctic hares in being solitary, or field work has been restricted to summer when the groups have split up. On study areas chosen because hares were numerous, Anderson (1974) recorded 23 hares on about 14km². The young behave like other hares, grunting and drumming with the feet (Walkinshaw 1947).

Reproduction

In West Alaska the breeding season starts in April and most young are born from 28 May to 14 June; there is only one litter a year and the mean litter size is 6.3 (3-8) with leverets at birth weighing 100g (Anderson and Lent 1977). The growth rate of young over the first ten weeks averaged 23.4g/day.

Status and Summary

The Alaskan hare is a rare species and seems to have decreased in numbers (Howell 1936). More work on distribution and numbers is required, although the habitat does not seem to be threatened.

Burmese Hare *Lepus peguensis* Blyth 1855

Subspecies: *Lepus peguensis peguensis*, *Lepus peguensis siamensis*, *Lepus peguensis vassali*

Description and Taxonomy

The Burmese hare is a smallish animal (2-2.5kg) closely allied to the Indian hare *L. nigricollis*. The back is reddish grey mixed with black, greyer on the rump, and the tail is black above, white below. The underparts are white and the rather large ears have a conspicuous black tip. The feet vary from white in the Burmese specimens to fulvous in those from Thailand.

The three subspecies may be conspecific with *L. peguensis* and all may be included in *L. nigricollis*.

Distribution

L. p. peguensis occupies the valleys of the Irrawaddy, Chindwin and Salween rivers from about 22°N to Rangoon (Wroughton 1915). *L. p. siamensis* is in Thailand where forest has been cleared (Lekagul and McNeely 1977) from Chiang-mai to Bangkok and south to 12°N in the Malay Peninsula (Gyldenstolpe 1917). *L. p. vassali* is in Laos, Cambodia and S. Vietnam to 225km south of Saigon (Van Peenan 1969). (See Fig. 4.10).

Habitat and Ecology

This species is a lowland hare, living on land cleared for crops and dry wasteland. In Malaya and S. Vietnam it occurs in sandy country along the coast and in Thailand on forest clearings in lalang grass or around hill tribe villages (Lekagul and McNeely 1977). There is no information on home range, population density or diet.

Behaviour and Reproduction

Apart from the casual references to its nocturnal habits, there is no information on behaviour. The only litter sizes quoted are one embryo (Gyldenstolpe 1917), two females with two embryos (Kloss 1919), and one litter of four (Pfeffer 1969).

Status and Summary

This species is represented by fairly small populations isolated from each other by forest. Their habitat is probably expanding as forests are cleared. More studies of taxonomy, distribution and behaviour are urgently needed, but the populations do not seem threatened at present.

Scrub Hare

Lepus saxatilis F. Cuvier 1823

Subspecies: *Lepus saxatilis albaniensis*, *Lepus saxatilis aurantii*, *Lepus saxatilis chiversi*, *Lepus saxatilis herero* (including *bechuanae*, *chobiensis*, *damarensis*, *khanensis*, *ngamiensis*), *Lepus saxatilis megalotis*, *Lepus saxatilis micklemi*, (including *gungunyanae*, *nigrescens*), *Lepus saxatilis orangensis*, *Lepus saxatilis saxatilis*, *Lepus saxatilis subrufus*, *Lepus saxatilis zuluensis*.

Description and taxonomy

The scrub hare is a large animal, averaging about 3.5kg (2-4kg) but shows a decrease in size from central south Cape Province to the northeast. It is now thought to merge with the African savanna hare *L. victoriae* (Robinson and Dippenaar 1987), a far smaller species (average 2kg) ranging from northern Cape Province to North Africa. The large South African form is pale buff-colored hare with greyer sides and white below; while the small northern form is darker grey on the back and the breast and flanks are rufous or chestnut, especially dark in high altitude specimens. There is also a distinct difference in ear length from 130-150mm in the large southern form to about 90mm in the north.

Taxonomically, the relationship of the scrub hare *L. saxatilis* and African savanna hare *L. victoriae* is still in dispute (Angermann and Feiler 1988) and in the long run all may be subspecies of the Indian hare *L. nigricollis*. For the present we separate *L. victoriae*, giving the ten subspecies above.

Distribution

The scrub hare occupies most of Cape Province, South Africa, excluding open grassland and dry desert. Taking the stepped

decline in ear length as the distinction between the scrub hare and the African savanna hare, the northeast boundary of its distribution is central Natal. It is commonest in southwest Africa, except in the Namib (Shortridge 1934). (See Fig. 4.9).

Habitat and Ecology

According to Shortridge (1934), the scrub hare is "partial to rocky or stony ground although its extensive range covers every type of country - open sandveld, bushveld, or forest." It is attracted by cultivation and garden crops, and has been recorded to dig out peanuts. There seems to be no detailed information on diet, home range or population densities.

Behaviour and Reproduction

The scrub hare is nocturnal, coming out at dusk to feed throughout the night. When disturbed by day it runs zigzag and lies up in cover again, and can be followed and put up several times (Shortridge 1934). It lies up on its own, but a second hare is often close; when both are flushed they run in different directions.

There has been no study of reproduction, but casual reports of newly born young are for May, October and November. Shortridge states there are probably two litters a year with two or three young in a litter. Bourquin and Sowler (1980) record breeding in October.

Status and Summary

The scrub hare appears to be common in Cape Province, but more data on population numbers and biology are desirable. Even if it is "only" a subspecies of the widespread African savanna hare, its large size and big ears remain to be explained. Regardless of taxonomy, this unusual form deserves attention.

Chinese Hare

Lepus sinensis Gray 1832

Subspecies: *Lepus sinensis flaviventris*, *Lepus sinensis formosus*, *Lepus sinensis sinensis*

Description and Taxonomy

The Chinese hare is small (1.25-1.94kg) and is a relatively richly colored animal with chestnut or rufous tones on the back and chest. The underparts are paler and the tail brown, giving the animal a rather uniform tone overall. The tips of the ears have black triangular markings. The fur is short, straight and somewhat coarse.

Taxonomically, this hare is distinct from other species in skull and tooth characters. It has been allied in the past with the Hainan hare *L. hainanus*, Japanese hare *L. brachyurus*, and the hispid hare *Caprolagus hispidus*, but none of these relationships is convincing. There are three subspecies (above). Many authors consider the Korean hare *L. coreanus* a subspecies of *sinensis*, but this does not seem established satisfactorily.

Distribution

Although the type location is near Canton, the present distribution according to Luo (1988) does not extend so far south, but only to about 23°N. Dao Van Tien (1978), on the other hand, lists the Chinese hare in northeast Vietnam. The northern boundary is the Yangtse River, and the southeast corner of mainland China is the main distribution area, from the coast to 107°E. In Taiwan hares are commonest in the south where there are more farms and early stages of forestry plantations (Shao-Pin Yo, pers. comm. 1981). (See Fig. 4.7).

Habitat, Ecology, Behaviour and Reproduction

There is very little published information about the Chinese hare. It appears to live on open waste-land and scrubby hills in southwest China rather than on rice fields. In Taiwan they are minor pests of forestry and are trapped in small numbers for sale in local markets (Shao-Pin Yo, pers. comm. 1981).

Status and Summary

More work is needed on the distribution and status of the Chinese hare. Its populations are likely to have become isolated by intensive agriculture in the highly populated areas it inhabits.

Ethiopian Highland Hare *Lepus starcki* Petter 1963

Description and Taxonomy

This is a medium-sized hare of about 2.53kg weight. The thick, soft fur on the back is tawny mixed with black, turning greyish towards the rump; the breast, sides, nape and legs are tawny and the underparts white; the overall effect is of rich contrasting colours somewhat similar to the European hare *L. europaeus*. The tails in the population at Shoa are entirely white, but in the Bale Mountains they have a black mid-dorsal stripe. The ear is multi-colored, with a brownish grey leading edge, pale grey over most of the back of the ear and a conspicuous black patch towards the tip which is not found in other East African hares.

The taxonomy is still unsettled. Petter (1963) described *starcki* as a subspecies of the Cape hare *L. capensis*, Angermann (1983) elevated it to a full species and Azzaroli-Puccetti (1987) considers it a relic population of the European hare *L. europaeus* dating from the late Quaternary. There are no named subspecies.

Distribution

The Ethiopian highland hare is restricted to the central plateau of Shoa Province, about 40km from Addis Ababa, and the mountains of Bale Province, from 2,500 to 4,000m above sea level. According to Angermann (1983) all locations are between 6°50' and 9°35'N, and 38° to slightly east of 40°E. (See Fig. 4.11).

Habitat, Ecology, Behaviour and Reproduction

Very little recorded. Dr. L. Brown (pers. comm. 1967) wrote:

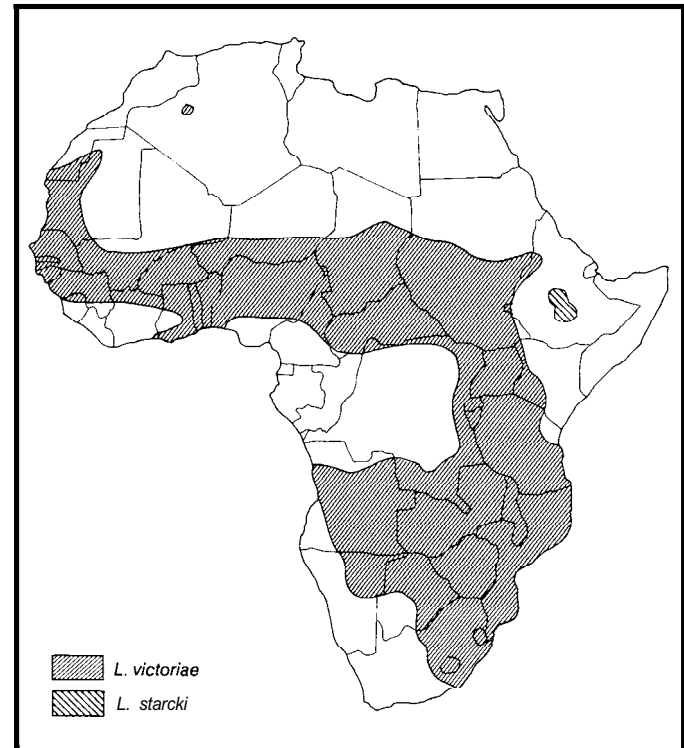


Figure 4.11 Distribution of the Ethiopian highland hare *Lepus starcki* and African savanna hare *L. victoriae*

“I have never seen so many, even on some Scottish moors, as there are in the heath zone of the Arussi Mountains in Ethiopia at over 11,000 feet. These could well be a new subsp...On the summit of the Arussi Mountains I found large brown eagles living on hares as a staple diet.”

Status and Summary

The Ethiopian highland hare appears to be relatively numerous, but more work is needed on its biology and habitat requirements. It deserves attention because of its restricted distribution.

Mountain Hare *Lepus timidus* Linnaeus 1758

Subspecies: *Lepus timidus abei*, *Lepus timidus ainu*, *Lepus timidus begitschevi*, *Lepus timidus canescens*, *Lepus timidus gichiganus*, *Lepus timidus hibernicus*, *Lepus timidus kolymensis*, *Lepus timidus kozhevnikovii*, *Lepus timidus lugubris*, *Lepus timidus mordeni*, *Lepus timidus orii*, *Lepus timidus scoticus*, *Lepus timidus sibiricorum*, *Lepus timidus timidus*, *Lepus timidus transbaicalicus*, *Lepus timidus varronis*.

Description and Taxonomy

This widespread species is very variable in size and color. Different populations average from two to four kilogrammes in weight and the summer coat can be pale grey or dusky brown in the mountains to rich rust-brown on the plains. In

general, the head tends to be browner than the body. The ears are black-tipped and shorter than the head. The tail is short and usually all white in both winter and summer, as are the underparts. There is a seasonal change to white winter pelage in autumn in all areas except Ireland, where only a few individual hares turn white or patchy. In spring they molt from white to a brown or grey summer coat and there is a third molt from brown to brown in late summer.

Following the separation of the mountain hare *L. timidus* and arctic hare *L. arcticus* (Baker *et al.* 1983) there are 16 subspecies.

Distribution

Mountain hares range from east Poland to the Pacific Ocean, from 75°N in the far north of Russia and Scandinavia, south to 40-50°N. There are isolated populations in Ireland, Scotland, Switzerland, Italy, the Kurile Islands and Hokkaido, Japan. It has been introduced into the Faeroes, England and various Scottish Islands; some introduced on Spitzbergen later died out. (See Fig. 4.10).

Habitat and Ecology

Mountain hares occupy tundra and open forest, particularly of pine, birch, and juniper. In Scotland and Ireland heather moors and bogland are favoured habitats, and in southern Russia copses in the middle of open steppe and reed belts around lakes. On agricultural land this species tends to be replaced by the European hare *L. europaeus* in Europe and the Cape hare *L. capensis* further east.



Mountain hare *Lepus timidus* on moorland in Scotland
(Photo by J.E.C. Flux)

The food eaten varies with the habitat. In Scotland and Ireland much heather *Calluna* is eaten, but this is not a major food in Europe where birch, juniper, poplar, willow and *Vaccinium* are favoured. Palatable grasses and clovers are taken when available.

Home ranges vary from 10-30ha in Scotland (Flux 1970, Hewson 1976) to 72 and 305ha for two hares tracked in Finland (Seiskari 1957). There is evidence of a three to four year cycle in abundance in Fenno-Scandia and a longer-term cycle of eight to twelve years in Scotland and Russia. Population densities are very variable: about 1-2 hares/km² over much of Sweden and Russia; 0.14/km² in west Scotland to 245/km² on the best areas in northeast Scotland (Watson and Hewson 1973); and on small islands such as Vedholmen in Sweden as high as 400/km² (Angerbjorn 1986).

Behavior

Mountain hares are nocturnal but there is increased daylight activity in summer when nights are short, or in winter when food is scarce. In snow, hares dig to reach vegetation and also make short tunnels for protection from adverse weather or aerial predators. They are more social than other hares and often gather to feed in the same place in groups of 20-100; one large group lives on the airfield in Belfast.

Reproductive behavior consists of a male (or small group of males) following 2-20m behind a female for hours, but the males seldom fight each other. In Europe mountain hares are reported to confuse their tracks before resting up for the day (Ognev 1966) but this has not been seen in Scotland (Flux 1970).

Reproduction

The gestation period of mountain hares is longer than in other leporids (47-55 days) and in Sweden first litters average 2.15 young and second litters 3.24 (Hoglund 1957). Superfoetation has not been recorded. In southern Norway and Scotland three litters can be produced giving an annual production of five to six young; in northern Russia there is only one litter of 6.4-6.9 young (Naumov and Shatalova 1974), but in the south three or even four litters can be born in a year (Gaiduk 1973).

At birth leverets weigh about 100g (61-182g) and grow at 14-30g per day. In captivity the young depend on milk for 10-20 days but those of the final litter may continue to suckle for six weeks (Flux 1970).

Status and Summary

Mountain hares are a very widespread and abundant species. They are regarded as vermin on grouse moors in Scotland and large numbers are shot in winter for export to Germany. In Russia many were harvested annually for skins, but this market has declined. In Ireland, Scotland and Japan they cause some damage to forestry plantations, while in Scandinavia they are a major game animal. Some subspecies may be threatened at present, e.g. those in the European Alps and central Italy, and more data on their population status is desirable.

White-tailed Jackrabbit
***Lepus townsendii* Bachman 1839**

Subspecies: *Lepus townsendii townsendii*, *Lepus townsendii campanus*

Description and Taxonomy

The white-tailed jackrabbit is greyish brown on the upper parts, white below and on the tail apart from a dusky or buff stripe on top. On the plains of British Columbia, Nebraska, Kansas and parts of Colorado they moult in winter into coats only a little paler, but elsewhere they turn almost completely white in winter, retaining only the black tips to the ears. The under-fur remains iron grey or reddish-brown (Hansen and Bear 1963). This hare is a little larger than the black-tailed jackrabbit, with adult males averaging 2.75kg and females 3.32kg in South Colorado (Bear and Hansen 1966) and 3.4kg and 3.59kg respectively in Iowa (Kline 1963).

There are two subspecies, *L. t. townsendii* to the east of the Rocky Mountains and *L. t. campanus* to the west. The species is well differentiated and there are no taxonomic problems of identification.

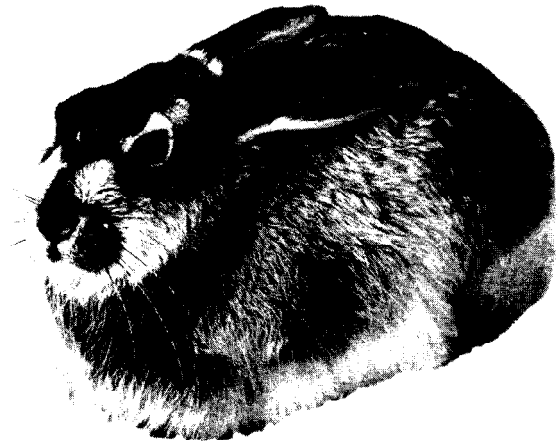
Distribution

The white-tailed jackrabbit has changed its distribution in historical times. In the early 1900s it was extending east as far as Wisconsin, Iowa and Missouri as forest was cleared, then, perhaps because of increasing cultivation of its prairie habitat, its range declined and it became extinct from Kansas and southern Nebraska in about 1950 (Dunn *et al.* 1982). It now occurs from mid Saskatchewan and Alberta to the north of Arizona, and from inland Washington and California to Lake Superior. (See Fig. 4.1).

Habitat and Ecology

The main habitat is open prairie and plains, but populations extend into the badlands of Dakota and on to montane pastures among scattered evergreens to 3,100m altitude in Colorado. In Iowa they are most numerous on recently glaciated soils, and less in the west (Kline 1963). In Southern Colorado Bear and Hansen (1966) rate the most favored habitats from grassland, sagebrush, rabbitbrush, to meadow. The meadows were used more in autumn following harvest, and in winter the use of shrubs for cover and open ridges for travel was noted. Early authors maintained that white-tailed jackrabbits adjusted well to agricultural development, but decline of numbers now seems general.

The diet in Colorado was 70% forbs, 19% grass and 7% shrubs in summer, changing to 76% shrubs and 12% forbs in winter (Bear and Hansen 1966). In North Dakota in spring they congregate on wheat and in summer, alfalfa (James 1967). Home ranges may be quite small (one measured at ten hectares, James 1967) but movements of one to two miles occur between cover and feeding grounds, and hares may have



White-tailed jackrabbit *Lepus townsendii* in snow form
(Photo by Dean E. Biggins, U.S. Fish and Wildlife Service,
F.T. Collins. Co.)

to migrate considerable distances in winter to avoid hard snow cover. In Iowa the average density was 5-15/sq. mile, with peaks of about 90-114 (Kline 1963).

Behavior

White-tailed jackrabbits are nocturnal, spending the day in forms and starting to feed at 15.00-16.00 hr; peak activity was at 22.00-01.00 hr, and most activity stopped by 03.00-04.00 hr in summer (James 1967). In winter they burrow for shelter into snow drifts and use shrubs and trees for cover. The hares then often congregate on favored feeding areas. Brunton (1981), for example, records a group of 30-150 feeding on a 300 x 400m patch of alfalfa for ten days in Alberta, with no sign of interactions between the feeding animals.

Reproduction

Courtship behavior is similar to that of the black-tailed jackrabbit, except that the jumping behavior is more pronounced (Blackburn 1973). In North Dakota the breeding season extends from late February through mid-July, females producing an average of 3.3 litters a year, with average litter size of 4.6 (1-9) (James and Seabloom 1969). In Iowa, Kline (1963) gives two to three or four litters a year, averaging 3.6 young per litter.

Status and Summary

The white-tailed jackrabbit is a widespread and apparently thriving species over much of central and western USA. It provides hunting for sport and is sold to fur buyers and mink ranchers. They are also regarded as pest of agriculture, especially on crops of alfalfa, corn, soybeans and winter wheat.

African Savanna Hare
***Lepus victoriae* Thomas 1893**

Subspecies: *Lepus victoriae angolensis*, *Lepus victoriae canopus*, *Lepus victoriae crawshayi*, *Lepus victoriae raineyi*, *Lepus victoriae victoriae*, *Lepus victoriae whytei*, *Lepus victoriae zechi*

Description and Taxonomy

The African savanna hare is of medium size, about 2kg (1.5 3kg). It tends to be more richly colored than the Cape hare *L. capensis*, with greyish brown back, rufous breast, sides and legs, and white below, but where the two species coexist in East Africa they may be almost identical in color (Flux and Flux 1983). Mountain forms are more rufous and darker in coloring. The ears are black towards the tip and the tail is black above, white below. The fur texture is coarser than in *L. capensis*.

Robinson and Dippenaar (1987) consider it conspecific with the scrub hare *L. saxatilis*, but for the present we follow Angermann and Feiler (1988) in treating them separately. The position of subspecies is unclear; we include those listed as "*crawshayi*" *sensu* Petter but exclude *L. fagani*.

Distribution

The African savanna hare occupies most of Africa south of the Sahara and north of South Africa, where it is replaced by the scrub hare *L. saxatilis*. There is an isolated population in South Algeria near Beni Abbes. (See Fig. 4.11).

Habitat and Ecology

The Cape hare coexists with the African savanna hare over much of its range. The separation seems largely by habitat, the Cape hare preferring more open, dryer country and the African savanna hare the scrubrier, more montane areas. In Ruanda-Urundi the African savanna hare likes *Themeda triandra* and *Imperata cylindrica* associations (Curry-Lindahl 1961), and in East Africa *Tarconanthus camphoratus* scrub (Flux and Flux 1983). Smithers (1971) measured the proportions of hares found in different vegetation types: 83% of Cape hares were in open grassland, 15% in scrub or woodland, while for African savanna hares the percentages were reversed.

The food eaten doubtless varies widely with the habitat. An intensive study in E. Africa by Stewart (1971) showed that the main plant items eaten were unidentified grasses (35%), *Digitaria* (19%) and *Hyparrhenia* (11%), while the Cape hare in the same area ate far less *Digitaria* and more *Themeda triandra*, and tended to graze closer to the ground.

There appear to be no measurements of home range of the African savanna hare, but from personal observation in East Africa they appear to have small ranges of 5-10ha. Population densities can be as high as nine hares/ha in Virunga National Park, Zaire, but averaged about 0.1-1.8/ha in 23 areas surveyed by Curry-Lindahl (1981). For the Serengeti, Frame and Wagner (1981) estimated a far lower density of 0.09 hares/ha,

which agrees with the 0.08/ha in good habitat in Uganda (Ogen-Odoi and Dilworth 1987).

Behavior.

African savanna hares in East Africa were normally solitary or seen feeding in groups of two or three in favoured areas. They were strictly nocturnal (Flux 1981b) and in Zaire Curry-Lindahl (1981) found that "a night count along 5km was 639 hares but at 09.00 next morning not a single animal was seen." This refers to road-counts, however, and Frame and Wagner (1981) record that hares could be raised in almost equal numbers day and night by a vehicle travelling cross-country. Hares in Uganda are attracted to cut grassland (Eltringham and Flux 1971) or the fresh growth produced after burning or overgrazing (Ogen-Odoi and Dilworth 1987).

Reproduction

In Botswana Smithers (1971) found that half to two-thirds of the adult females examined were pregnant in all months of the year. A similar pattern of continuous breeding occurred in Uganda (Flux 1981a). Mean litter sizes were likewise similar, averaging 1.6 in both Botswana and Uganda. The annual production of young would average about eight per female.

Status and Summary

The African savanna hare is a widespread, successful species over much of Africa. Isolated populations, such as that at Beni Abbes in southern Algeria, deserve attention.

Yarkand Hare
***Lepus yarkandensis* Gunther 1875**

Description and Taxonomy

The Yarkand hare is a small species of about 1.4kg (1.1-1.9kg). The head and body are a uniform sandy brown color with a pinkish tint in summer, the sides sand yellow and the underparts white. The top of the tail is the colour of the back, without the usual black hairs of many *Lepus*. The ears are long and lack the black tips also. In winter the color is much paler. In general appearance the Yarkand is closest to *L. capensis tolai* but seems to be a distinct desert species (Angermann 1967b). There are no recognized subspecies.

Distribution

The Yarkand hare is restricted to the Tarim Basin, Xinjiang, between latitudes 36-42°N and longitudes 76-92°E. It has a circular distribution in a ring round the Taklamakan desert, relying on vegetation near the streams descending from the surrounding mountains (Gao 1983, Luo 1988). (See Fig. 4.7).

Habitat and Ecology

The preferred habitat is Chinese tamarisk or poplar forest and brushwood along the margins of the rivers, which produce "islands" of vegetation as they run into the desert. Other vegetation such as reedy meadows can be used, but the hares

tend to avoid agricultural fields.

The hares eat grass and crops, causing some damage to melons. There is no information on home range, but Gao (1983) records that four men in the field for three hours could each encounter 20 or more hares, indicating a reasonably high population density.

Behaviour and Reproduction

Yarkand hares are mainly nocturnal and are usually seen in the early morning or late evening. They make shallow runways in the vegetation under bushes. Up to six individuals may congregate at one place on a river bank to drink (annual rainfall in this area is between 4.5 and 76mm).

There is little information on reproduction. The litter size is usually two (up to five). A pregnant female was shot in May and a newly-born young seen in September.

Status and Summary

Yarkand hares are shot as a game animal and about 10,000 furs are produced annually (1958 to 1981) with little sign of decline. Although the population would decline with more intensive agriculture, the present system of allowing fields to revert to scrub from time to time enables hares to persist (Gao Yaoting, pers. comm. 1989). Nevertheless, this species deserves attention because of its restricted habitat and distribution.

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Chapter 5: The Cottontails

Joseph A. Chapman and Gerardo Ceballos

Status and Summary

The cottontails (genus *Sylvilagus*) comprises 13 species. However, some believe there are 14 species in two subgenera; *Sylvilagus* and the monotypic *Brachylagus*. All *Sylvilagus* are New World forms and reach their greatest diversification in North America. The swamp rabbit *S. aquaticus*, Audubon's cottontail *S. audubonii*, brush rabbit *S. bachmani*, eastern cottontail *S. floridanus*, Nuttall's cottontail *S. nuttalli* and marsh rabbit *S. palustris* are important game species managed by state wildlife agencies in the United States. The forest rabbit *S. brasiliensis*, although widely distributed, is poorly known over much of its range, thus more information is needed about this species. The Mexican cottontail *S. cunicularius* is found over a large region in west central Mexico, where viable populations are located in many areas, and should be considered out of danger. Status surveys are recommended for Dice's cottontail *S. dicei* and the San Jose brush rabbit *S. mansuetus*. The Tres Marias *S. graysoni* and the Omilteme *S. insonus* cottontails are recommended for endangered status.

Overview

Cottontails are widely distributed throughout North, Central and the northern half of South America. The most widely distributed member of the genus is the eastern cottontail. It inhabits diverse habitats from southern Canada to northern South America. Other species have smaller distributions, with some found only on islands as insular forms (i.e. the San Jose brush rabbit and Tres Marias cottontail). The forest rabbit is the most successful of the southern forms. Its distribution extends from southern Mexico into northern Argentina and it is the only member of the genus occurring south of the equator.

Cottontails are true rabbits, with altricial young born naked in a nest or "form". Cottontails vary in size from the small pygmy rabbit (approx. 400g) to the largest member, the swamp rabbit (approx. 2,000g). Most are darkly colored on the back and light below. All cottontails have relatively large ears and feet. The skull of *Sylvilagus* is typically rabbit-like, with a highly fenestrated maxillary bone, a straight cutting edge on the upper incisors, and a second set of "peg" teeth posterior to the upper incisors. The presence of an interparietal bone distinguishes the genus *SyZviZagus* from the genus *Lepus*. The females are from one to ten per cent larger than

males in most *Sylvilagus* (Chapman, et al 1982).

Phylogenetic relationships have received considerable attention in recent years. The dendrogram in Fig. 5.1 is a composite of the systematic relationship among the ten species of *Sylvilagus* for which cytological data are available (Holden and Eabry 1970, Diersing and Wilson 1980, Robinson et al. 1983, 1984, Lorenzo et al. in press).

Seven of the 13 species of *Sylvilagus* apparently share a common ancestral link. The swamp rabbit and the marsh rabbit are closely related, as are the eastern cottontail, the Tres Marias cottontail and the Mexican cottontail (the last three forms share a basic diploid number of 42). Audubon's and Nuttall's cottontails are also closely related to each other. Cytological and morphological information suggests that the Tres Marias cottontail is more closely related to the Mexican cottontail than to the eastern cottontail (Diersing and Wilson, 1980; Lorenzo et al., in press).

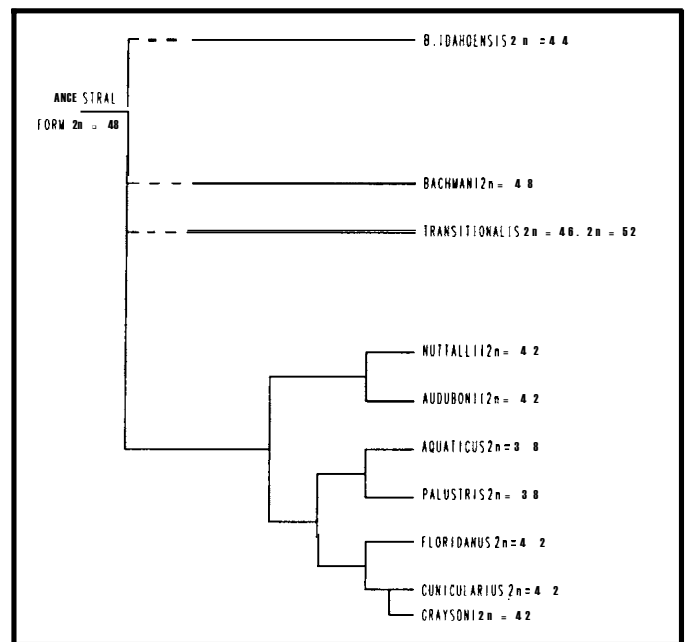


Figure 5.1 Composite dendrogram of the systematic relationships among the North American cottontails (*Sylvilagus* and *Brachylagus*). The basic dendrogram is taken from Robinson et al. 1984 and modified using material from Holden and Eabry 1970, Diersing and Wilson 1980, Robinson et al. 1983 and Lorenzo et al. in press.

No single vegetative community can be identified as cottontail habitat. Their habitat requirements are met in numerous diverse locations. Cottontails inhabit a wide variety of disturbed, successional and transitional habitats, often characterized by forbs and perennial grasses, with an abundance of well-distributed escape cover such as sage brush (*Artemisia* sp.), bramble (*Rubus* sp.) or Frailejones (*Espeletia* sp.). Cottontails have high rates of reproduction and their populations are regulated through mortality and dispersal. Escape cover is essential to their habitat requirements.

Population levels vary markedly between species and from year to year, depending on climate, habitat type and other factors. Local populations of the eastern cottontail have reached unusual densities of more than ten per ha. Densities of one to five per ha are probably the norm. In desert species such as Audubon's cottontail, densities of less than one rabbit per ha are more normal.

Cottontail behavior is stereotyped and fairly consistent with other rabbit species. Both non-social behavior, including basic postures, movements and vocalizations, and adult social behavior largely centered on reproductive interactions have been documented (Marsden and Holler 1964, Tefft and Chapman 1987).

The number of young produced annually by *Sylvilagus* varies among species, with an elevational and latitudinal gradient within species. Cottontails are iteroparous. The eastern cottontail is the most fecund member of the genus often producing 25-35 young per year, while the forest rabbit appears to be the least fecund, producing about ten young per year (Durant 1981, Chapman et al. 1982, Chapman 1984).

In general, cottontails are cyclic in abundance, thus long term trends are more useful in assessing their status than population levels in any one year. Even with the eastern cottontail, the most common species in North America, long-term declines in numbers probably occur. Habitat is the key to cottontail abundance. According to Chapman et al. (1982:99); "We can expect weather-related, local and short-term population increases, but the basic pattern (of population decline) will continue unless there is a major agricultural recession that leads to less intensive land use... Conservationists and wildlife managers should strive to develop and preserve grassland habitat whenever possible on public and private lands. The true plight of grassland animals such as the cottontail is only beginning to be appreciated". Despite the continued loss of cottontail habitat to agriculture and development, cottontails remain the most important game animals in North America (Chapman, et al. 1982). In those species with limited or patchy distributions, or which live in island habitats, such as the Tres Marias cottontail, Omilteme cottontail or New England cottontail, habitat protection is critical.

The biology and status of the 13 species of cottontails in the subgenus (*Sylvilagus*) are discussed below in detail. The genus was reviewed by Chapman et al. (1982).

Species Accounts

Swamp Rabbit

Sylvilagus aquaticus (Bachman 1837)

Subspecies: *Sylvilagus aquaticus aquaticus*, *Sylvilagus aquaticus littoralis*

Description and Taxonomy

The swamp rabbit is the largest member of the genus *Sylvilagus* (wt 2000g). Its back is blackish to rusty brown in color. The belly and underside of the tail are white. The species possesses a prominent cinnamon-colored eye-ring. Unlike other members of the genus, sexual dimorphism is not pronounced.

There are two subspecies of *S. aquaticus*. The more northern form *S. a. aquaticus* is found associated with mature forests, while the southern form *S. a. littoralis* is found associated with coastal and riparian areas. Detailed range maps are in Chapman and Feldhamer (1981).

Distribution

The swamp rabbit is found in the southeastern United States. (Fig. 5.2), including the states of Alabama, Louisiana, Mississippi, Texas, Oklahoma, Kansas, Missouri, Illinois, Indiana, Tennessee, Georgia and South Carolina.

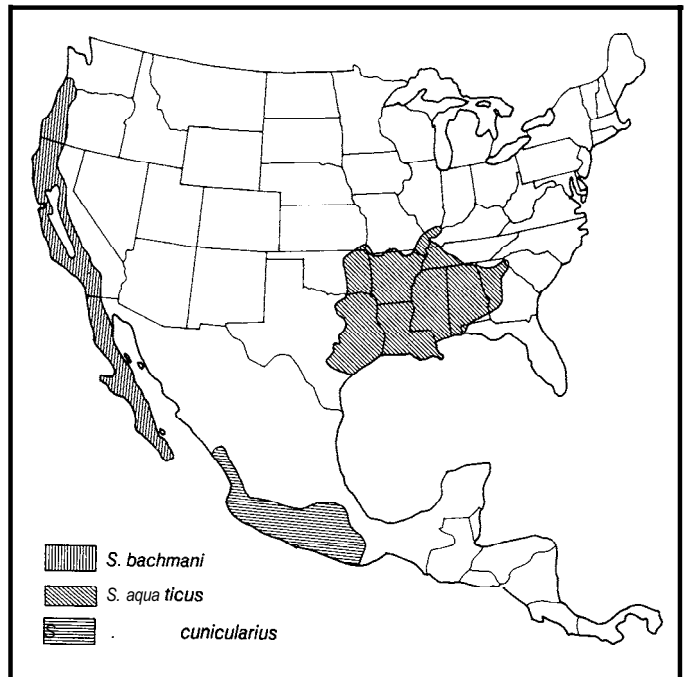


Figure 5.2 Distributions of the swamp rabbit *Sylvilagus aquaticus*, brush rabbit *S. bachmani* and Mexican cottontail *S. cunicularis*

Habitat and Ecology

The swamp rabbit is a subtropical species found in swamps, river bottoms and lowland areas. Its distribution in the north is limited to the southern swamp forest community-type at about the 24°C isotherm. Swamp rabbits are always associated with water (Lowe 1958, Hunt 1959, Terrel 1972). In the northern portion of their range, swamp rabbits are found in mature forests and regenerating forest tracts 15 years old (Terrel 1972), and in canebrake communities (Harrison and Hickie 1931). Much of this habitat has been eliminated. The swamp rabbit subspecies *S. a. aquaticus* has begun to decrease in the northern part of its range in the United States, apparently due to habitat alteration and riparian drainage. In Missouri, swamp rabbit habitat decreased from 850,000ha in 1870 to less than 40,000ha in 1973 as a result of the conversion of lowland hardwood forests to row crops (Korte and Fredrickson 1977). Despite the shrinkage of swamp rabbit habitat on the periphery of the range, there are still large areas of prime habitat in states such as Louisiana where they remain important game animals. Recent studies indicate a home range of about 0.5 and 1.0ha for female and male swamp rabbits, respectively. Densities in timbered habitat were estimated at two rabbits per ha (Kjølhaug and Woolf 1988).

Swamp rabbits feed on a variety of grasses, forbs and sedges. Their preferred food items appear to be *Carex* and other sedges (Toll *et al.* 1960, Terrel 1972).

Behavior

Swamp rabbits exhibit a linear dominance hierarchy among males that does not include females. They form breeding groups of several animals controlled by a dominant male. The male hierarchy has been characterized by: (1) less overt aggression between conspecific males during reproduction activities, (2) restriction of dominant-subdominant challenges between adult males, (3) a direct relationship between social status and frequency of male dominance displays, (4) a direct relationship between male social status and male-female interactions. Swamp rabbits are highly territorial and males may maintain their dominant status from year to year (Marsden and Holler 1964, Holler and Sorenson 1969, Sorenson *et al.* 1972).

Reproduction

The breeding season of the swamp rabbit varies throughout its range and from year to year. In the northern portion of their range the breeding season usually starts in February (Hill 1967). In the south they apparently breed year-round (Hunt 1959). Litter size varies from one to six. Females may produce two to five litters per year (Sorenson *et al.* 1968).

Status and Summary

Although there has been some reduction in its range, the swamp rabbit remains an abundant and important game species in the Gulf states. As a game species, its harvest is regulated by various state wildlife agencies. No additional conservation measures are needed. The species has been reviewed by Chapman and Feldhamer (1981).

Audubon's or Desert Cottontail *Sylvilagus audubonii* (Baird 1857)

Subspecies: *Sylvilagus audubonii arizonae*, *Sylvilagus audubonii audubonii*, *Sylvilagus audubonii baileyi*, *Sylvilagus audubonii cedrophilus*, *Sylvilagus audubonii confinis*, *Sylvilagus audubonii goldmani*, *Sylvilagus audubonii minor*, *Sylvilagus audubonii neomexicanus*, *Sylvilagus audubonii parvulus*, *Sylvilagus audubonii sanctidiegi*, *Sylvilagus audubonii vallicola*, *Sylvilagus audubonii warreni*

Description

The Audubon's cottontail is relatively large for the genus *Sylvilagus* (weight 1,000g). The ears are long and sparsely haired on the inner surface. The tail is large and the feet sparsely haired. The upper body and tail are gray, the underside white. There are 12 subspecies.

Distribution

The species is found from near the Canadian border in Montana, south into central Mexico and from the Pacific coast of California, east into central Texas, Oklahoma, Kansas, Nebraska, South Dakota and North Dakota (Fig. 5.3). Detailed range maps for the subspecies are in Chapman and Willner (1978).

Habitat and Ecology

The Audubon cottontail is an inhabitant of arid regions, occurring from below sea level in Death Valley, California to at least 1,829m in mountainous regions (Orr 1940). It may be

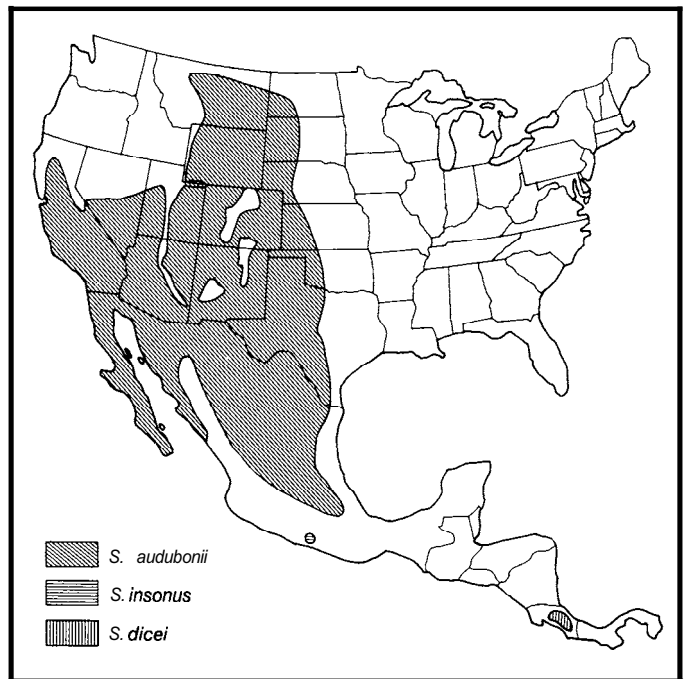
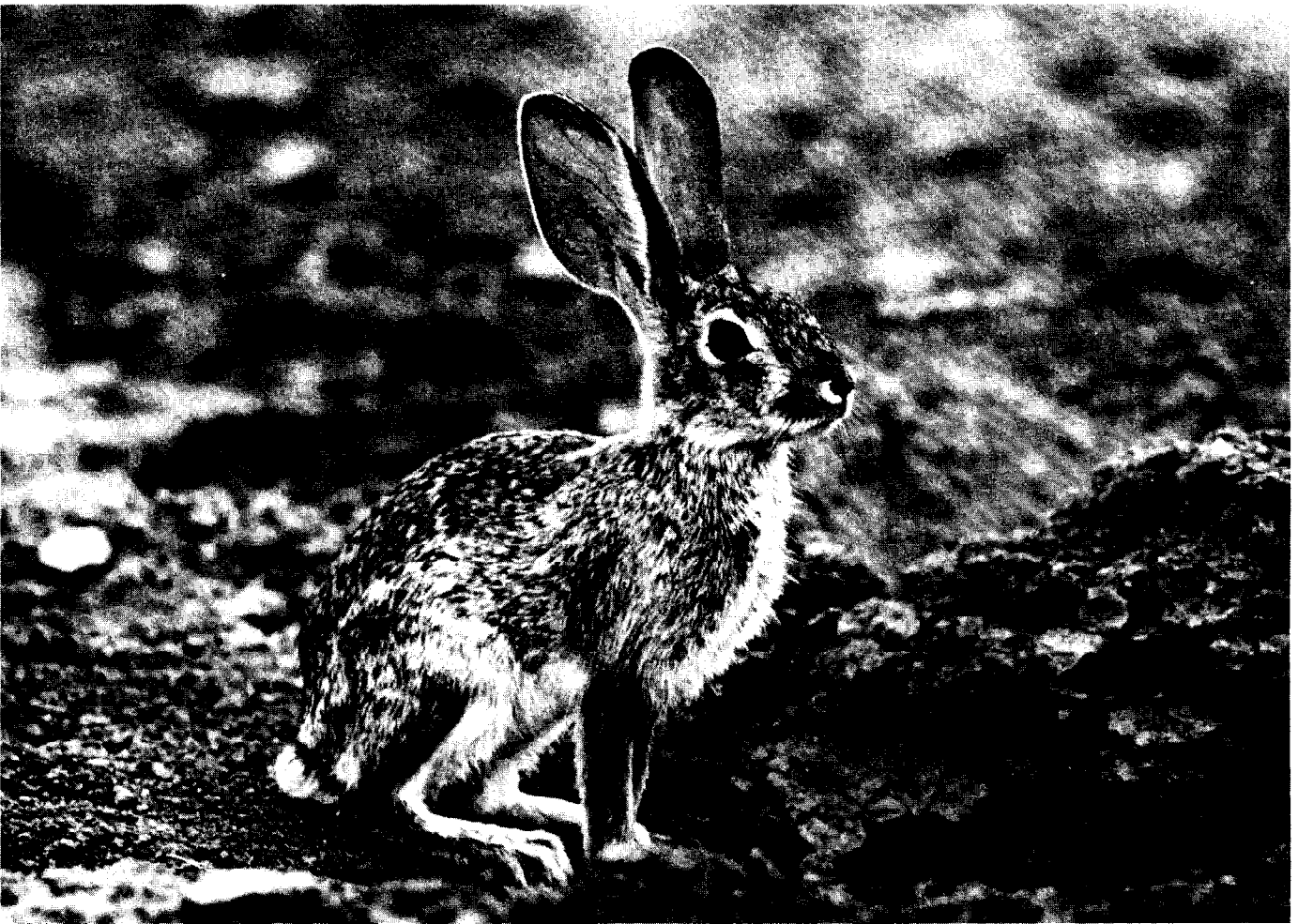


Figure 5.3 Distribution of Audubon's cottontail *Sylvilagus audubonii*, Dice's cottontail *S. dicei*, and Omilteme cottontail *S. insonus*



Audubon's cottontail *Sylvilagus audubonii* (Photo by Leonard Lee Rue III)

found in woodlands, grasslands and deserts at lower elevations throughout the southwestern United States (Findley 1969). The species is frequently found associated with riparian zones in arid regions.

Behavior

There have been no studies dealing directly with the behavior of Audubon's cottontails, however, some behavioral observations have been made. They are most active in the evening and early morning and inactive at temperatures above 80°F (Ingles 1941) . This cottontail is not gregarious, uses low prominences such as stumps as lookout posts (Orr 1940) and may climb trees (Summer 1931, Ingles 1941).

Reproduction

The length of the breeding season varies from year-round to seven months depending on location. Usually, the breeding season begins in December or January and extends for seven to nine months. Litter sizes are small for the genus, averaging 2.6 to 3.6 young per litter (Orr 1940, Sowls 1957, Chapman and Morgan 1974).

Status and Summary

The Audubon cottontail is an important game species and its status is monitored in many states. Land clearings and cattle grazing may effect Audubon cottontail population levels



Habitat of Audubon's cottontail *Sylvilagus audubonii* at Sonora, Mexico (Photo by G. Ceballos)

(Kundaeli and Reynolds 1972, Flinders and Hansen, 1975). In Mexico it is still common over much of its geographic range. None of the twelve subspecies is known to be under threat and no additional conservation measures are required.

Brush Rabbit

Sylvilagus bachmani (Waterhouse 1838)

Subspecies: *Sylvilagus bachmani bachmani*, *Sylvilagus bachmani cinerascens*, *Sylvilagus bachmani cerrosensis*, *Sylvilagus bachmani ubercolor*, *Sylvilagus bachmani exiguus*, *Sylvilagus bachmani mariposae*, *Sylvilagus bachmani virgulti*, *Sylvilagus bachmani howelli*, *Sylvilagus bachmani macrorhinus*, *Sylvilagus bachmani peninsularis*, *Sylvilagus bachmani riparius*, *Sylvilagus bachmani tehamae*, *Sylvilagus bachmani rosaphagus*

Description and Taxonomy

The brush rabbit is one of the smaller cottontails (weight up to 1,000g). The color of the back is dark brown to gray brown, while the belly and underside of the tail is whitish. The feet are small and sparsely haired. The legs, ears and tail are short.

There are 13 recognized subspecies, which are discussed in detail in Chapman (1974).

Distribution

The brush rabbit is confined to the Pacific coast, from the Columbia River in the north to the tip of Baja California in the south. It does not occur east of the Cascade/Sierra Nevada Mountain Ranges (Fig. 5.2). Its range has not changed appreciably in historic times.

Habitat and Ecology

Brush rabbits require dense bramble clumps (*Rubus*) or other thick brushy habitat (Orr 1940, Chapman 1971). These bramble clumps often have an extensive network of trails and runways. The species will occasionally use burrows, but does not dig its own. The home range is very small (less than 2,000m²) depending on the uniformity of the habitat (Shields 1960, Chapman 1971). Brush rabbits eat mainly edible grasses (Orr 1940), but also will take berries and other vegetation (Chapman 1974).

Behavior

The behavior of the brush rabbit has not been quantified although some behavioral observations have been made (Orr 1940, Zoloth 1969). Brush rabbits are extremely cautious when venturing from dense cover to feed. They exhibit a minimum individual distance of 0.3-8m (1-24ft) without an aggressive "chase" resulting. Nose touching and sniffing often precede a "chase". The species also exhibits stereotype grooming behavior (Zoloth 1969). Brush rabbits may climb low shrubs and trees, a behavior unusual in the Leporidae (Chapman 1974). In Oregon, the introduced eastern cottontail *S. floridanus* was reported to exhibit aggressive behavior toward the brush rabbit (Chapman and Verts 1969).

Reproduction

The breeding season varies from north to south. In Oregon, breeding begins in February and ends in August (Chapman and Harman 1972), while in California it begins in December and ends in May or June (Mossman 1955). Litter size also varies between regions. The average litter size was 2.8 in Oregon, 3.5 in northern and central California and 4.0 in west central California (Orr 1940, Mossman 1955, Chapman and Harman 1972). The brush rabbit is one of the less fecund members of the genus, producing about 15 young in five to six litters per year (Chapman and Harman 1972).

Status and Summary

The brush rabbit is a game species in both Oregon and California, but is hunted little. There is no detailed information on its status in Baja California, but it is still quite abundant. No additional conservation measures are proposed. The species was reviewed by Chapman (1974).

Forest Rabbit or Tapeti

Sylvilagus brasiliensis (Linnaeus 1758)

Subspecies: *Sylvilagus brasiliensis andinus*, *Sylvilagus brasiliensis appollinaris*, *Sylvilagus brasiliensis brasiliensis*, *Sylvilagus brasiliensis canarius*, *Sylvilagus brasiliensis capsalis*, *Sylvilagus brasiliensis caracsensis*, *Sylvilagus brasiliensis chillae*, *Sylvilagus brasiliensis chotamus*, *Sylvilagus brasiliensis consobrinus*, *Sylvilagus brasiliensis defilippi*, *Sylvilagus brasiliensis fulvescens*, *Sylvilagus brasiliensis gabbi*, *Sylvilagus brasiliensis gibsoni*, *Sylvilagus brasiliensis inca*, *Sylvilagus brasiliensis kelloggi*, *Sylvilagus brasiliensis meridensis*, *Sylvilagus brasiliensis mimensis*, *Sylvilagus brasiliensis paraquensis*, *Sylvilagus brasiliensis peruanus*, *Sylvilagus brasiliensis sanctaemartae*, *Sylvilagus brasiliensis surdaster*, *Sylvilagus brasiliensis tapetillus*, *Sylvilagus brasiliensis truei*



Habitat of the forest rabbit *Sylvilagus brasiliensis* in a tropical rain forest at Los Tuctlas, Veracruz, Mexico (Photo by G. Ceballos)



Figure 5.4 Distribution of the forest rabbit *Sylvilagus brasiliensis*

Description and Taxonomy

The forest rabbit is a small to medium-sized rabbit with a markedly small to rudimentary tail, short hind feet and very short ears. Its color ranges from light grey to almost black dorsally, slightly lighter on the sides of the body and the tail, and a whitish belly except for a dark throat patch. The tail is dark ventrally.

There are 23 recognized subspecies of the forest rabbit (Johnson and Chapman in press). However, the species is in need of systematic revision (see Diersing 1981 and Chapman and Johnson in press for examples).

Distribution

The forest rabbit occurs as far north as southern Tamaulipas, Mexico, southward along the eastern coast of Mexico and the Yucatan Peninsula (Quintana Roo, Yucatan and Campeche) to western Guatemala. It probably occurs southward to El Salvador. It does occur in Honduras, the eastern half of Nicaragua, eastern Costa Rica and Panama. Forest rabbits occur throughout South America except at high altitudes above snow line and in the Patagonian region south of the Argentine **Chaco** (Fig. 5.4). Little is known about the species distribution in the Amazonian Region (Hershkovitz 1950, Diersing 1981, Chapman and Willner 1982, Chapman and Johnson in press).

Habitat and Ecology

Although widely distributed, the forest rabbit has been studied in some detail only in the **Paramos** of Venezuela (Durant, 1981, 1983). In Mexico and Central America this species is mainly found in tropical forests, including rain, deciduous and

second growth forests; it also occurs in pastures near forested habitats. In Los Tuxtlas, Veracruz, a representative habitat of the species in Mexico, the rain forest includes a well-developed canopy, with trees up to 50m high such as *Brosimum alicastrum* and *Nectandra ambigens*, and a sparse understory.

Behavior

The forest rabbit builds elaborate above-ground nests to rear its young. The nests are built of dry grasses and consist of a central chamber, with three to four small chambers at the end of a runway system (Durant 1981, Chapman and Willner-Chapman 1982).

Reproduction

In Chiapas, Mexico, this species reproduces throughout the year. The gestation period is around 28 days and the litter size is between three and eight (Alvarez del Toro 1977). In the **Andean Paramos**, the forest rabbit breeds year-round. They have a long gestation of 44 days and produce an average of 4.7 litters per year (*S. b. meridensis*). The mean litter size is 1.2, the smallest average litter-size reported for the genus (Durant 1981, 1983). Annual production of young is less than ten per year.

Status and Summary

In northwestern South America, habitats of the forest rabbit and the eastern cottontail *S. floridanus* appear to be mutually exclusive. Forest rabbits cling to dwindling forests and clearings within them and to the **Paramos** of the **Andean** crests. Cottontails are replacing forest rabbits in artificial savannas cutting through the original forests. Undoubtedly, the larger, more prolific and aggressive cottontail, together with the predators which follow it, is the most important factor contributing to the exclusion of the forest rabbit from the ever-expanding artificial savannas and scrublands of northwestern South America.



The forest rabbit *Sylvilagus brasiliensis meridensis*
(Photo by J. A. Chapman)



Figure 5.4 Distribution of the forest rabbit *Sylvilagus brasiliensis*

Description and Taxonomy

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There are 23 recognized subspecies of the forest rabbit (Johnson and Chapman in press). However, the species is in need of systematic revision (see Diersing 1981 and Chapman and Johnson in press for examples).

Distribution

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Reproduction

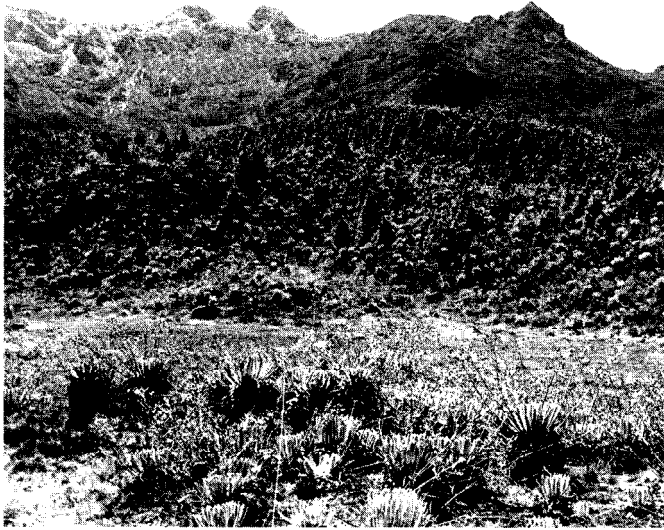
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The forest rabbit *Sylvilagus brasiliensis meridensis*
(Photo by J. A. Chapman)



Habitat of the forest rabbit *Sylvilagus brasiliensis meridensis* in the Paramo de Mucabaji, Merida, Venezuela. The plant in the foreground is frailejones *Espeletia schultzii* a common plant of the Venezuelan Paramo (Photo by J. A. Chapman)

However, little knowledge is available regarding the impact of tropical deforestation on the abundance of this species. In Mexico, the abundance of the forest rabbit apparently declines when extensive areas are deforested. However, it survives well in second growth forests and pastures (Alvarez del Toro 1977). A systematic survey is needed to elucidate the status of the forest rabbit over much of its range. The South American forms of this species were reviewed by Chapman and Johnson (in press).

Mexican Cottontail

Sylvilagus cunicularius (Waterhouse 1848)

Subspecies: *Sylvilagus cunicularius cunicularius*, *Sylvilagus cunicularius insolitus*, *Sylvilagus cunicularius pacificus*

Description and Taxonomy

The Mexican cottontail is large for the genus (weight 1,800-2,300g). The fur is coarse and brownish gray to reddish above, to white underneath.

Three subspecies of *S. cunicularius* are recognized (Hall 1981).

Distribution

The Mexican cottontail is found in the coastal lowlands of the Pacific coast and in the temperate forests of Central Mexico, including the states of Sinaloa, Nayarit, Jalisco, Colima, Michoacan, Guerrero, Oaxaca, Distrito Federal, Mexico, Morelos, Tlaxcala and Puebla (Fig. 5.2). It occurs from sea

level to 4,300m in Central Mexico (Leopold 1959; Ceballos and Galindo 1984, Armstrong and Jones 1971).

Habitat and Ecology

The Mexican cottontail occurs in temperate forests in central Mexico and in tropical dry deciduous and semi-deciduous forests in western Mexico (Leopold 1959, Ceballos and Galindo 1984, Ceballos and Miranda 1986). In central Mexico it is quite abundant in the pine and pine-oak forests with a dense cover of "zacatoness" (bunch grasses; genera *Agrostis*, *Festuca* and *Muhlenbergia*). Extensive habitat is found along the mountains of the Transvolcanic belt, especially in the Popocatepetl, Iztaccihualt, Pelado and Nevado de Toluca volcanoes. In the mountains south of Mexico City it is microsympatric with two other species of rabbits (eastern cottontail *S. floridanus* and volcano rabbit *Romerolagus diazi*).

In western Mexico it is found in dry deciduous forests and pastures, but is more abundant in pastures and other disturbed vegetation (Ceballos and Miranda 1986). In southern Sinaloa southward to western Michoacan, the Mexican cottontail occurs along the coastal plain from sea level to the mountain slopes. In the mountain slopes is parapatric with the eastern cottontail (Diersing and Wilson 1980).

Reproduction

The species is iteroparus and reproduction occurs throughout the year.

Status and Summary

Although this species has declined in some areas because of overgrazing, hunting, or the destruction of its habitat, it is still quite abundant throughout its geographic range. No additional conservation measures are required.

Dice's Cottontail

Sylvilagus dicei Harris 1932

Description and Taxonomy

A large-bodied cottontail, with dorsal pelage a mixture of black and brown, blackish-gray sides, rudimentary blackish tail and whitish venter except for a brownish throat patch (Diersing 1981). No subspecies are recognized.

Distribution

Dice's cottontail is found in the higher elevations of Costa Rica and western Panama. According to Diersing (1981) it occurs from 3,800m at Cerro Chirripo to no lower than 1,640m at Cervantes, Costa Rica. In Panama it occurs to 1,180m at Rancho de Rio Jimenez (Fig. 5.3).

Status and Summary

Little is known about the biology, ecology or status of this species. A status survey is needed.

Eastern Cottontail
***Sylvilagus floridanus* (J.A. Allen 1890)**

Subspecies: *Sylvilagus floridanus alacer*, *Sylvilagus floridanus ammophilus*, *Sylvilagus floridanus avius*, *Sylvilagus floridanus aztecus*, *Sylvilagus floridanus chapmani*, *Sylvilagus floridanus chiapensis*, *Sylvilagus floridanus cognatus*, *Sylvilagus floridanus connectens*, *Sylvilagus floridanus continentis*, *Sylvilagus floridanus costankensis*, *Sylvilagus floridanus cumanicus*, *Sylvilagus floridanus floridanus*, *Sylvilagus floridanus hesperius*, *Sylvilagus floridanus hitchensi*, *Sylvilagus floridanus holzneri*, *Sylvilagus floridanus hondurensis*, *Sylvilagus floridanus illanensis*, *Sylvilagus floridanus mallurus*, *Sylvilagus floridanus margaritae*, *Sylvilagus floridanus meamsi*, *Sylvilagus floridanus nelsoni*, *Sylvilagus floridanus nigronuchalis*, *Sylvilagus floridanus orinoci*, *Sylvilagus floridanus orizabae*, *Sylvilagus floridanus paulsoni*, *Sylvilagus floridanus purgatus*, *Sylvilagus floridanus restrictus*, *Sylvilagus floridanus robustus*, *Sylvilagus floridanus russatus*, *Sylvilagus floridanus similis*, *Sylvilagus floridanus subcinctus*, *Sylvilagus floridanus superciliaris*, *Sylvilagus floridanus valenciae*, *Sylvilagus floridanus yucatanicus*

Description and Taxonomy

The eastern cottontail is a large member of the genus *Sylvilagus* (weight 1,300g). The fur is long and dense, grayish to brownish on the upper parts and white on the venter and tail. The South American forms have a nuchal patch varying from black to yellowish-brown, depending on subspecies.

There are 34 recognized subspecies of eastern cottontail (Chapman *et al.* 1980). However, the species is in need of systematic revision. There are five insular subspecies that are probably of recent origin, introduced by man, and of questionable subspecific status. These include *S. f. ammophilus*, *S. f. hitchensi*, *S. f. avius*, *S. f. margaritae* and *S. f. nigronuchalis*. The remainder are mainland subspecies.



Eastern cottontail *Sylvilagus floridanus*
 (Photo by Jerry Focht, Leonard Rue Enterprises)

Distribution

The eastern cottontail occurs over broad geographic provinces from southern Canada to northwestern South America (Fig. 5.5) (Chapman, *et al.* 1980). The species has been widely transplanted in North America and Europe. It is an aggressive species (Chapman and Verts 1969) and may displace other Leporids.

Habitat and Ecology

The eastern cottontail is usually thought of as a mammal of farmland, fields and hedge rows; however, historically it was found in natural glades and woodlands, deserts, swamps, prairies, hardwood forests, tropical savannas, rain forests and boreal forests. Its range overlaps that of six species of *Sylvilagus* and six species of *Lepus*. Genetic studies of widely separated populations of the eastern cottontail indicate considerable intraspecific genetic variability within the species (Chapman and Morgan 1973, Morgan and Chapman 1981). This genetic variability may be related to the wide range of habitats the species occupies.

The eastern cottontail has been the subject of widespread introduction programs, especially in the eastern United States. These introductions have permanently altered the gene pool of the eastern cottontail (Chapman and Morgan 1973), appear to have made the species a highly efficient colonizer and may have contributed to the species' ability to displace sympatric cottontails, such as the New England cottontail *S. transitionalis*.

Eastern cottontails have relatively large home ranges. Home ranges of both sexes averaged about three hectares in Wisconsin (Dixon *et al.* 1981). However, home range size varies significantly depending on season, sex, age and individ-

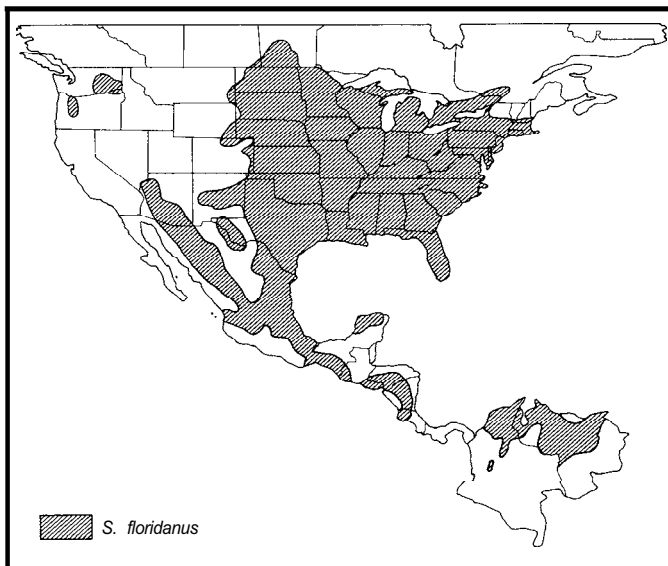


Figure 5.5 Distribution of the eastern cottontail *Sylvilagus floridanus*

ual rabbits (Chapman and Tretheway 1972). Peak densities of eight to ten rabbits per hectare have been recorded (Trent and Rongstad 1974, Bittner and Chapman 1981), but densities are normally much lower. Eastern cottontails feed on a wide variety of plants depending on the season and geographic location.

Behavior

The behavior of the eastern cottontail has been studied more than most other members of the genus (Marsden and Conway 1963, Marsden and Holler 1964, Bruch and Chapman 1983). However, much of the work has been descriptive in nature. The eastern cottontail exhibits two major categories of social behavior (1) basic postures, movements and vocalizations and (2) adult social interactions, which include reproductive interactions and dominant-subordinant interactions. As discussed earlier, eastern cottontails have a male dominance hierarchy which controls the social structure of their populations.

Reproduction

Onset of annual reproduction varies from population to population and from year to year, depending on weather, latitude and elevation. Diet and rainfall also appear to be important factors, especially in arid regions (Bothma and Teer 1977). Litter size varies, from 3.0 to 5.6. Five to seven litters per female have been reported as well as juvenile female breeding (Chapman et al. 1982). Annual production of young may reach 35 kittens per year under ideal climatic conditions.

Status and Summary

The eastern cottontail is the most important game animal in the United States (Chapman et al. 1982) and the species has been the subject of hundreds of research projects and publications. It has been widely introduced in North America and many island populations are probably of recent origin. The species has also been introduced into Europe, a practice which should be stopped (Sasse 1983). The species was reviewed by Chapman et al. (1980) and Chapman (1983).



Habitat of eastern cottontail *Sylvilagus floridanus* in Allegany County, Maryland, USA (Photo by J. A. Chapman)

Tres Marias Cottontail *Sylvilagus graysoni* (J.A. Allen 1877)

Subspecies: *Sylvilagus graysoni badistes*, *Sylvilagus graysoni graysoni*

Description

The Tres Marias cottontail is similar in appearance and size to the eastern cottontail *S. floridanus*. However, it is confined to the Tres Marias Islands, off Nayarit, Western Mexico, and there is no chance of confusing the two allopatric species. These rabbits are brownish to reddish dorsally, brownish to pale reddish on the sides, and whitish on the venter except for a brown throat patch (Diersing and Wilson 1980).

Distribution and Taxonomy

The species is endemic of the Tres Marias Islands, Nayarit, Mexico (Fig. 5.6). This group of continental islands is approximately 86km from mainland Nayarit. Two subspecies have been recognized: *S. g. graysoni*, found in the islands of Maria Madre, Maria Magdalena and Maria Cleofas, and *S. g. badistes*, found only in San Juanito island.

The species is closely related to the Mexican rabbit *S. cunicularius* of the adjacent mainland. Both species are morphologically very similar and have the same diploid chromosome number of 42 (Diersing and Wilson 1980, Lorenzo et al., in press). Diersing and Wilson (1980) suggested that the ancestors of *S. graysoni* invaded the Tres Marias Islands, that were very likely connected to the mainland during the maximum Pleistocene glaciation. The hypothesis that the islands and mainland were connected is supported by the presence of freshwater fishes on the islands.

Habitat and Ecology

The dominant vegetation formations of Tres Marias Islands are the tropical dry deciduous and moist forests, which are characterized by a dense cover, with many tree species. The Islands are used by the Mexican government as a high security prison and the presence of large numbers of people has resulted in extensive disturbance there. On Maria Madre and Maria Cleofas, large areas of the natural vegetation have been destroyed by local inhabitants. House rats *Rattus rattus* were accidentally introduced to all the Islands and white-tailed deer *Odocoileus virginianus* and domestic goats were deliberately introduced on Maria Magdalena. Introduced species have caused profound changes in the ecological conditions of the Islands, that are likely to cause (or have caused) strong impacts on the native wildlife.

In a field survey done by D. E. Wilson in 1976, the Tres Marias cottontail was relatively more abundant on the uninhabited islands (Maria Cleofas and San Juanito). However, about half of the vegetation of Maria Cleofas has now been cleared in preparation for settlement (Dooley 1987, pers. comm.). Maria Magdalena has recently been designated an Ecological Reserve by the Mexican government.

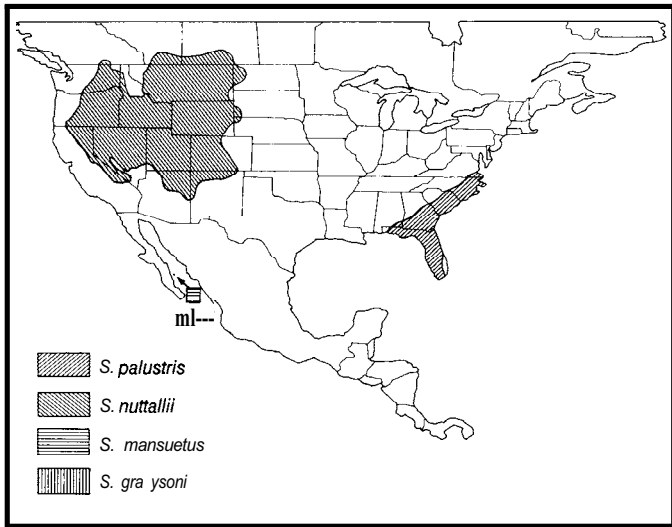


Figure 5.6 Distribution of the Tres Marias cottontail *Sylvilagus graysoni*, San Jose brush rabbit *S. mansuetus*, Nuttall's cottontail *S. nuttallii* and marsh rabbit *S. palustris*

Behavior

According to Wilson (1987, pers. comm.) these "rabbits are amazingly tame and easy to shoot."

Status and Summary

The Tres Marias cottontail is recommended for endangered status because of extensive habitat alterations on the Tres Marias and San Juanito Islands. Major threats are introduced species that compete for food, alter the native vegetation and prey upon the rabbits, and habitat destruction by inhabitants. This recommendation is supported by recent expeditions to the islands by the Oxford University (Dooley 1987, pers. comm.), the U.S. National Museum of Natural History (D.E. Wilson 1987, pers. comm.) and the National University of Mexico (Ceballos and Navarro, in press).

Additionally, a detailed, long-term study to identify the current status and basic biological characteristics of this species is strongly recommended.



100000

Skin of Omilteme cottontail *Sylvilagus insonus*
(Photo by Don E. Wilson)

Omilteme Cottontail *Sylvilagus insonus* (Nelson 1904)

Description and Taxonomy

This is a large cottontail with a short tail, medium-sized hindfeet and long ears. The back is rufous in color and tinged with considerable black. The sides are grayish-black, the tail is reddish-black dorsally, the venter is dingy white except for a brownish throat patch, the hindfeet show considerable white dorsally (Diersing 1981). No subspecies of the Omilteme cottontail *S. insonus* are recognized.

Distribution

The species is known from less than ten specimens. It occurs only in the Sierra Madre del Sur, in the vicinity of Omilteme, Guerrero, Mexico, at elevations between 2,300m and 5,280m (see Fig.5.3).

Habitat and Ecology

The species is restricted to pine and pine-oak forests in the abrupt mountains of the Sierra Madre del Sur. Vegetation near Omilteme, the type locality, is dominated by pine forests with temperate elements such as *Pinus*, *Quercus* and *Anus*; there are, however, cloud forests with tropical species in the deep "barrancas." The Omilteme cottontail occurs sympatrically with the eastern cottontail *S. floridanus*.

Status and Summary

S. insonus is one of the least known cottontails. It is recommended for endangered status because it has an extremely narrow distribution (<500km²) and it is quite rare (see also Ceballos and Navarro, in press). For example, none were seen in a recent year-long survey of the mammals from Omilteme by the National University of Mexico (J. Juarez, pers. comm.). Although Omilteme has been recently declared a State Reserve by the Mexican government, major threats to this cottontail are hunting and habitat destruction. The coniferous forests have been highly modified and fragmented by intense forestry and cattle grazing. Additionally, this species is of high priority for a status survey.

San Jose Brush Rabbit *Sylvilagus mansuetus* Nelson 1907

Description and Taxonomy

The San Jose brush rabbit *S. mansuetus* is an insular species closely related to the brush rabbit *S. bachmani*. The species resembles the brush rabbit but is lighter in overall color. Cranial features are most useful in separating these two species. No subspecies are recognized.

Distribution and Ecology

Found only in San Jose Island, Gulf of California, Baja California, Mexico (Fig. 5.6). San Jose island (194km²) is one of the largest islands of the California Gulf, probably originated

in the Pliocene, and is separated by five kilometres from mainland Baja California. Its arid vegetation is dominated by cacti and other succulent plants (Case and Cody 1983). Only six other native species of mammals are found on the island, but cats and rats have been accidentally introduced.

Status and Summary

Little is known about the biology, ecology or status of the San Jose brush rabbit. Thus, this species is of high priority for a status survey.

Nuttall's or Mountain Cottontail *Sylvilagus nuttallii* (Bachman 1837)

Subspecies: *Sylvilagus nuttallii grangeri*, *Sylvilagus nuttallii nuttallii*, *Sylvilagus nuttallii pinetis*

Description and Taxonomy

Nuttall's cottontail is small to medium in size (weight 850g). The ears are short and rounded at the tip. The legs are long for the genus and the feet are covered with long, dense hair. The back is grayish and the belly is white. The tail is large and grizzled in color.

Three subspecies of *S. nuttallii* are recognized. A detailed range map is presented in Chapman (1975).

Distribution

Nuttall's cottontail occurs in the intermountain region of North America (Fig.5.6). A recent northward expansion of this species' range into southern British Columbia has been noted by Cowan and Hatter (1940). In California, Nuttall's cottontail occurs from 1,500m to at least 3,450m (Orr 1940). The eastern cottontail *S. floridanus* has displaced Nuttall's cottontail over much of the latter's former range in southeastern North Dakota (Genoways and Jones 1972).

Habitat and Ecology

The habitat of Nuttall's cottontail varies considerably over its range. The species is primarily associated with sagebrush *Artemisa* sp. in the north, while in the southern part of its range it occurs in timbered areas (Hall 1951). Nuttall's cottontail is commonly associated with rocky, brushy and wooded areas (Orr 1940, Hall 1951). This cottontail uses both burrows and forms (Orr 1940); however, they apparently do not dig their own burrows.

Populations of Nuttall's cottontail vary in density from 0.06 to 2.5 per ha in shrub-juniper scrublands in central Oregon



Nuttall's or mountain cottontail *Sylvilagus nuttallii* (Photo by Irene Vandermolen)

(McKay and Verts 1978) and they appear to feed primarily on sagebrush. However, in the spring and summer grasses are selected (Orr 1940) .

Reproduction

The onset and duration of the breeding season varies within the range of the species. In northeastern California, it begins in April and lasts into July (Orr 1940). In central Oregon the breeding season lasts from mid-February to the end of July (Powers and Verts 1971). In California each female normally produces two litters (Orr 1940) whereas four or five litters appear to be the norm in Oregon (Powers and Verts 1971). Average litter size is about four to six (range 1–8) and varies between locations within the species range (Orr 1940, Powers and Verts 1971). In Oregon, an adult female breeding throughout the reproduction season could produce 22 young per year. Juvenile breeding appears to be rare (Powers and Verts 1971) .

Behavior

Nuttall's cottontail appear to be more solitary than other *Sylvilagus*. Its solitary nature may be attributed to the uniform, often sagebrush, habitat in which it is found. When disturbed the rabbit will usually run 5-15m into cover, then pause, with ears held erect. Feeding usually occurs in brush, or at least near cover (Orr 1940).

Status and Summary

Nuttall's cottontail is a common game species throughout the intermountain west of the United States. It is managed by state and provincial wildlife agencies, primarily through hunting seasons and bag limits. The species has been reviewed by Chapman (1975).

Marsh Rabbit

Sylvilagus palustris (Bachman, 1837)

Subspecies: *Sylvilagus palustris hefneri*, *Sylvilagus palustris paludicola*, *Sylvilagus palustris palustris*

Description and Taxonomy

The marsh rabbit is a large (1.1-1.6kg) dark brown rabbit with rough hair. Its feet are reddish-brown above, darker below. The small tail is inconspicuous and whitish below.

Three subspecies are recognized, *S. p. paludicola*, *S. p. palustris* (Chapman and Willner 1981) and *S. p. hefneri* (Lazell 1984).

Distribution

The marsh rabbit is found from the Dismal Swamp, Virginia, south along the coastal lowlands into the Florida Keys (Fig. 5.6).

Habitat and Ecology

The marsh rabbit is confined to marshy habitats. They are

most often found associated with brackish water areas, although historically have been found around freshwater marshes as well. They are often found associated with cattails *Typha* sp. and, unlike other leporids, the most important factor limiting their distribution is the availability of water (Blair 1936).

Behavior

Like many leporids, the marsh rabbit is nocturnal, spending much of the day resting in a form. Marsh rabbits are at home in the water and swim well. The species usually walks, rather than hopping about in rabbit fashion. Their home range is considered small (Tompkins 1935, Blair 1936).

Reproduction

Marsh rabbits breed year round. Approximately six litters are produced per year per adult female. Mean litter size is approximately three. Annual production of young ranges from 15 to 20.

Status and Summary

Very little is known about marsh rabbit biology and ecology. The species is considered a pest in some prime agricultural settings; however, the insular subspecies *S. p. hefneri* which occurs only on the Florida Keys, Monroe Co., Florida (Lazell 1984) has recently been listed as an endangered subspecies (Federal Register Vol. 55, No. 120; 25588). The species was reviewed by Chapman and Willner (1981). The taxonomic status of this species needs evaluation.

New England Cottontail

Sylvilagus transitionalis (Bangs 1895)

Description and Taxonomy

The New England cottontail is a medium to large rabbit (weight up to 1,000g). The dorsal body parts are pinkish buff to ochre in color. The back is overlain with distinct black hair. The ears are short and rounded and possess a distinct black edge. There is a distinct black spot between the ears, but never a white spot as may occur in the eastern cottontail *S. floridanus*. Because of the similarity in appearance of the New England and eastern cottontails, pelage characteristics are not always diagnostic. Cranial characteristics are the most reliable means of distinguishing the two species (Chapman and Morgan 1973, Chapman 1975). No subspecies of the New England cottontail are recognized.

Distribution

The New England cottontail occurs in a mosaic pattern from southeastern New England south along the Appalachians to Alabama (Fig. 5.7). Chapman and Stauffer (1981: 978-979) suggested that the New England cottontail is a refugial relict. Further, they hypothesized that "this mosaic distributional pattern resulted from a gradual change in the climate coupled with the reinvasion of lowland areas by *S. floridanus*." The



The New England cottontail *Sylvilagus transitionalis*
(Photo by K. B. Fuller)

process appears to be continuing in the northern Appalachians and is being accelerated by habitat alteration (Chapman and Stauffer 1981) .

Habitat and Ecology

The New England cottontail is confined to the ericaceous vegetation zone of the Appalachian Mountains and New England. Chapman and Stauffer (1981) have postulated that much of their habitat is being invaded by populations of the eastern cottontail. The disappearance of New England cottontail throughout much of the northeastern USA has been documented by Linkkila (1971) . The species is considered rare in Maryland but relatively abundant in certain portions of West Virginia where large blocks of suitable habitat still remain (Chapman and Morgan 1973).

In New England, habitat preferences of the New England and eastern cottontails were difficult to distinguish (Linkkila 1971, Johnston 1972, Jackson 1973). No clearly identifiable habitat type could be associated with either species. However, Jackson (1973) attributes the decline of the New England cottontail to natural succession. More recently, Hoff (1987:89) reported that in "Southeastern Massachusetts where maximum relief is less than 100m, the species has retreated to more cold, wet patches."

In the mid-Atlantic region, the eastern cottontail is confined to the higher elevations of the Appalachian mountains (Llewellyn and Handley 1945, Barbour 1951, Chapman and Morgan 1973, Blymyer 1976). The regions were characterized by presence of clear cuts, overgrown farmsteads or pockets of heath-conifer habitat. The common characteristic was dense cover and conifers.

In the southern Appalachians, New England cottontails are confined to mountain balds or areas of conifers and

scrubby vegetation such as *Kalmia*, *Vaccinium* and *Rhododendron*. The relationships between this vegetation, latitude and elevation are apparent (Chapman and Stauffer 1981) .

The New England cottontail feeds on a variety of vegetation, but is the only species of cottontail which may feed extensively on conifer needles (Spencer and Chapman 1986).

Behavior

The behavior of the New England cottontail was studied by Tefft and Chapman (1987). They divided the behavioral repertoire of this species into non-social and social behavior. Non-social behavior included commonly observed activities of lone rabbits. Social behavior included basic postures, vocalizations, movements, reproductive interactions and dominant-subordinate interactions of young and adult males and females.

The basic behavior patterns of this cottontail were stereotyped and ritualized and similar to those reported for many other Leporidae. Access to females and reproduction are regulated by a dominance hierarchy in males. Reproductive behavior is most intense during the estrus period of females, with little social interaction occurring between estrus periods. Reproductive behavior begins two to three days before parturition and post-partum breeding (Tefft and Chapman 1987).



Figure 5.7 Distribution of the New England cottontail *Sylvilagus transitionalis*

Reproduction

The reproductive biology of the New England cottontail has been studied in Maryland and West Virginia (Chapman et al 1977). The breeding season of the species lasts from early March to early September, the peak being between March and July. New England cottontails are **post-partum** synchronous breeders. Juvenile breeding of females accounts for nearly 20% of the pregnancies. The litter size is about 3.5 and the average annual production of young is about 24 per female.

Status and Summary

The status of the New England cottontail has been of concern to biologists and resource agencies for nearly two decades. In 1979, Chapman and Stauffer (1981) suggested to the IUCN/SSC Lagomorph Specialist Group that the species be listed in a classification of special **concern**. Their recommendation was based on the fact that the species appears to differ significantly from the more common eastern cottontail, with which it shares much of its range. Considerable new information has been collected since 1979 and several States have begun to consider carefully the status of the New England cottontail (Feldhamer et al. 1984, Fies and Coggin 1985, MacCallum 1985, Hoff 1987). Of interest are the differences which may exist between the demes of this species, in particular the differences between the two cytotypes. The species has a northern cytotype (2N = 52) and a southern cytotype (2N = 46) (Holden and Eabry 1970, Robinson et al. 1983, Ruedas 1986). The species was reviewed by Chapman (1975).

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Chapter 6 : The Pygmy Rabbit *Brachylagus idahoensis*

Frederick C. Dobler and Kenneth R. Dixon

Status and Summary

The pygmy rabbit *Brachylagus idahoensis* (Merriam 1891) is locally threatened in parts of its range. In Washington state, there remains only a small disjunct population which is currently being considered by the state for listing as endangered. In other parts of its range, particularly in southeastern Idaho, it is secure, with healthy populations remaining in areas of expansive habitat. In California, where it is considered a species of concern, it is classified as a game animal and included in the open hunting season.

The primary threat to the species results from the fragmentation of the sagebrush rangeland by sagebrush removal, which isolates populations, particularly on the edges of the range of the species. As the "islands" of habitat are made smaller, local extinctions may occur. The probability of extinction increases through overgrazing, wildfire, habitat modification or genetically related stochastic events. These local extinctions add up to a reduction of the species distribution.

Description

Body size of the pygmy rabbit is the smallest of any North American rabbit species. Orr (1940) reported a mean body weight of 409g (375-435g) for six adult males and 398g (246-

458g) for nine adult females from California. In Utah, Janson (1946) found six adult males averaged 405g (373-428g) and four adult females averaged 436g (415-456g). The mean weights of males and females in Idaho were 418g and 462g, respectively, according to Wilde (1978).

The grayish coat is long and silk-like when new; the abdomen is white; and the legs, chest and nape are cinnamon buff. Ears are short, rounded and thickly haired both inside and out. The tail is small: 15-20mm in males and 15-24mm in females (Orr 1940, Janson 1946). The underside is distinctively buff-colored compared to the white underside found in cottontails.

Distribution

The pygmy rabbit is found throughout much of the sagebrush area of the Great Basin as well as some of the adjacent intermountain area (Fig. 6.1) (Green and Flinders 1980a). The eastern boundary extends to southwestern Montana and western Wyoming (Campbell et al. 1982). The southeastern boundary extends to southwestern Utah (Janson 1946, Pritchett et al. 1987) and includes the only occurrence of the species outside the limits of the Pleistocene Lake Bonneville (Columbia River) drainage. Central Nevada (Nelson 1909) and northeastern California (Orr 1940) form the southern and western boundaries. The northern boundary of the main population historically reached to the southern foothills of the Blue Mountain Plateau (Bailey 1936) in eastern Oregon. Weiss and Verts (1984) found that the distribution had shrunk southward toward the central part of eastern Oregon (Fig. 6.1).

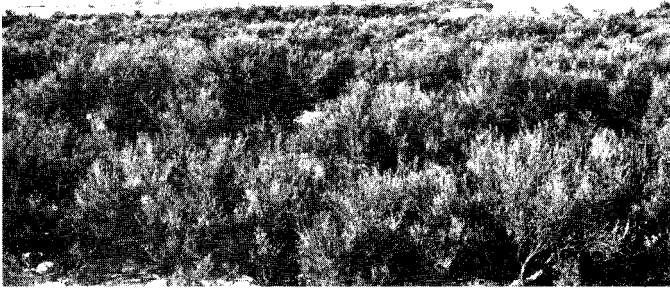
Within its range, its occurrence is far from continuous. Even in good habitat in southeastern Idaho, it is found only in the denser sagebrush/bitterbrush patches (46% cover), avoiding areas of lower sagebrush density (26-30% cover) (Green and Flinders 1980b). In Oregon, where the values for percentage cover were lower than in Idaho, the habitat preference was again for denser sagebrush (Weiss and Verts 1984).

The northern extent of its range is Douglas County Washington. The Washington population is disjunct from the rest of the range of the species and likely has been for some time. Butler (1972) stated that the pygmy rabbit has declined from its postglacial population high, which occurred more than 7,000 years ago. Habitat change likely accounts for this decline in numbers and the isolation of the Washington population.

In Washington, the pygmy rabbit was found historically in several areas in the Columbia Basin (Couch 1923), including collections at seven sites. However, much of the once exten-



Adult pygmy rabbit *Brachylagus idahoensis*
(Photo by Christopher Garber)



Pygmy rabbit habitat in Douglas County, Washington
(Photo by Christopher Garber)

sive sagebrush (shrub-steppe) in eastern Washington has been removed for agriculture or has been heavily grazed. Recent visits to these historic sites have so far produced evidence that only one of these populations still exists. In some cases the sagebrush has been eradicated. In 1987 the rabbit was found in Douglas County in two separate locations, both on private land. The first was near Burton Draw and the second along Coyote Canyon. Prior to this recent verification, its continued presence in Washington was undocumented. The last previous sighting in Washington was in 1979. In 1989, pygmy rabbits were also found near a site last collected in 1948 at Sagebrush Flat, also in Douglas County. This site is on state land managed by the Washington Department of Natural Resources.

Habitat

The pygmy rabbit is largely dependent upon sagebrush (primarily big sagebrush, *Artemisia tridentata*), but is usually found in areas where big sagebrush grows in very dense stands. Within stands of sagebrush it selects sites that have the



Pygmy rabbit habitat near Dubois, Idaho
(Photo by Christopher Garber)

greatest cover densities. Orr (1940) stated that tall sagebrush clumps were essential and contemporary studies corroborate this observation.

In Idaho, Green and Flinders (1980b) found that shrub cover and height were significantly greater in sites selected by pygmy rabbits. They found both bitterbrush *Purshia tridentata* and big sagebrush present in equal amounts (19% cover) on six pygmy rabbit sites. The combined shrub density was 46%. The mean shrub height for the sites selected by pygmy rabbits was 56cm; the mean height for all other sites was 25cm. In Oregon, Weiss and Verts (1984) found that mean shrub cover density on occupied sites was 28.8% with sagebrush species accounting for 23.7% of the cover. Mean shrub height at pygmy rabbit sites in Oregon was 84cm. Mean shrub cover on unoccupied sites was 17.7% and mean height was 53cm. While the values reported by the two studies were not the same, partly a product of different measurement techniques, both studies reported that high cover density appeared to be a major habitat feature selected by pygmy rabbits.

The density of big sagebrush in areas used by pygmy rabbits exceeds that which is found throughout most of the plant's distribution. In Washington the areas chosen are those which have been disturbed in the past by either grazing or cultivation. Usually heavy grazing increases the density of big sagebrush (Ellison 1960). After grazing has ceased and the grass cover has recovered, the habitat becomes optimal for pygmy rabbits. One site in Washington had been cultivated and then abandoned years ago. Big sagebrush invaded the fields and provided a dense cover of regrowth of sagebrush.

Blaisdell(1953) says that the sagebrush association in pre-settlement times was likely an open stand of shrubs with a highly diversified understory of perennial grasses and forbs. Christensen (1963) in Utah found that where bunchgrass vegetation has not been subjected to disturbance, big sagebrush is rarely the leading dominant. Mean density of big sagebrush in pre-settlement times was probably about 10-15% cover, much lower than that selected by the pygmy rabbit (2846%). This suggests that the pygmy rabbit is an opportunist, inhabiting disturbed sites in the sagebrush landscape which have an increased density of sagebrush. In some natural, non-disturbed situations, sagebrush density may exceed 20%, but these sites are rare and limited to areas where soil moisture is greater. Pygmy rabbits may be somewhat self-sustaining, however, increasing the density of sagebrush near their burrow sites (Janson 1946, Wilde 1978) by their feeding activity (Pearson 1965). The area around an active pygmy rabbit site is heavily grazed by the rabbits.

The burrowing habit of the pygmy rabbit (Hall 1946, Janson 1946, Severaid 1950, Jones 1957, Wilde 1978, Green 1978, Green and Flinders 1980a) is unique among the western North American rabbits. Burrows are usually under big sagebrush and only rarely located in an opening in the vegetation, reinforcing the dependence of this rabbit on sagebrush clumps (Green 1978, Green and Flinders 1980a, Wilde 1978). Because it makes its own burrows, soil structure is thought to be a key habitat feature. Generally soft, deep soils are re-

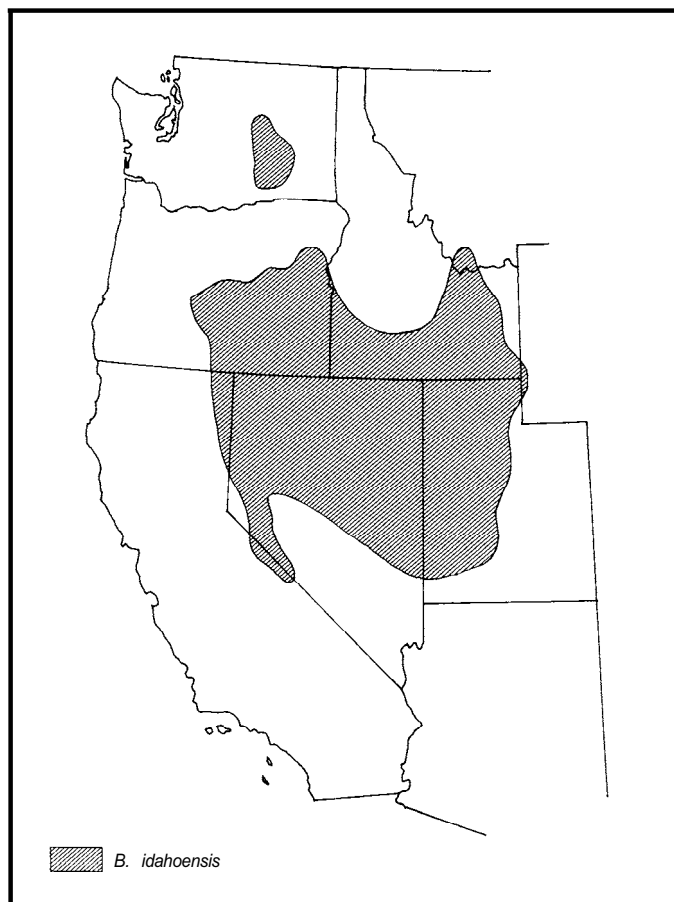


Figure 6.1: Range of the pygmy rabbit (adapted from Green and Flinders 1980a)

quired for burrowing. Wilde (1978) states that “they will live only where soil is deep enough and of a certain quality.” Alluvial fans may provide the soil requirement in some cases (Orr 1940, Green and Flinders 1980a). Weiss and Verts (1984) found that Oregon burrow sites were located where soil was significantly deeper and looser than at adjacent sites. Wilde (1978) examined burrow placement and found indications that rabbit burrows were placed where wind-borne soil deposits were deeper. Our studies and Green and Flinders’ (1980a) show that the pygmy rabbit also uses holes in volcanic rock, rock piles and around abandoned buildings. Usually these cases are in association with a population using typical deep soil, sagebrush burrow sites and may only be an energy-efficient alternative to digging a burrow, or may give added protection against predators that excavate the burrows.

Topography also plays a part in burrow site selection beyond the deposition of soil. The rabbits use the contours of the soil, most often digging into a slope (Wilde 1978, Dobler unpubl.). Even when they use level sites, they often utilize a small rise or change in contour for the burrow entrance.

Ecology

The population dynamics of the pygmy rabbit are not well understood. The best information on the population structure is provided by Wilde (1978). He showed that the average age of females tended to be greater than that of males. Because his study lasted only two and one-half years, however, the oldest observed age class was three years old. He found that mean annual adult mortality was as high as 88%. The period of greatest mortality began in January and extended through March. The survival of juveniles was initially very low, with more than 50% disappearing within five weeks of emergence. In one year of his study, 100% of the third cohort of reproduction perished.

Our studies in Washington, as well as studies in Idaho (Wilde 1978), showed that coyote *Canis latrans* and badger *Taxidea taxus* prey upon pygmy rabbits and may dig up many burrows. In Idaho, Wilde (1978) reported that weasels *Mustela frenata* frequently kill trapped pygmy rabbits and implied that they may enter burrows to prey upon them as well. Gashwiler *et al.* (1960) reported that pygmy rabbits are part of the diet of bobcats *Lynx rufus* in some areas. Raptors that also prey upon pygmy rabbits include the great horned owl *Bubo virginianus*, long-eared owl *Asio otus* (Borell and Ellis 1934, Hall 1946, Ingles 1965) and the northern harrier *Circus cyaneus* (Wilde 1978, Janson 1946, Green 1978, Green and Flinders 1980a).

Wilde (1978) reported that the minimum number of rabbits known to be alive on his study area reached a high of 67 in the fall and winter. He did not compute this into a density, but his study sites covered an area in excess of 300 hectares. Janson (1946), using flushing transects and burrow counts, estimated densities between 0.7 and 1.4 per hectare. These estimates are much lower than the estimate reported by Green (1978) of 45 per hectare in ideal habitat. Although Green did not say how the value was computed, it may represent a smaller area than the other estimates. B. Keller (pers. comm.) suggested that the pygmy rabbit is cyclic. Green and Flinders (1980a), however, do not agree. While there do appear to be fluctuations in the size of populations, more work is needed to determine if these fluctuations are cyclic.

The home range size of the pygmy rabbit has never been determined. Although Wilde (1978) did study movements with radiotelemetry, he made no estimate of home range and simply stated that the rabbits did not leave the area during his study. Janson (1946) observed feeding activity within a 27m radius of the burrow in the winter and reported that the area increased in the spring. Dobler (unpubl.) followed one set of tracks in fresh snow over 250m from an area of fresh digging to an active burrow site. Green and Flinders (1979) found that an escaped captive had returned to its burrow of origin 2.6km from the holding pen. This may be circumstantial evidence that the rabbit was familiar with an area inclusive of the holding pen site.

Behavior

The pygmy rabbit makes extensive use of burrows and may be unique in that it usually digs its own burrow (Borell and Ellis 1934, Severaid 1950, Walker et al. 1964). The burrows usually have several entrances; Janson (1946) reported that in Utah four or five were typical, but ten have been observed. In Idaho, two entrances were most often found (Wilde 1978). Entrances are 10-12cm in diameter and usually found at the base of a large sagebrush on a gentle slope. Tunnels usually extend to no more than one metre in depth.

The species is reported to be crepuscular (Davis 1939, Janson 1946), but may be found above ground any time of day. A study in Idaho showed the peak of activity to be during mid-morning (Bradfield 1975). Pygmy rabbits generally are found within a 30m radius of their burrow during winter, with an expanded home range in spring and summer (Janson 1946). They have a rather deliberate gait, staying low to the ground. To avoid predators, they may depend more on their ability to maneuver through dense sagebrush than on speed (Merriam 1891, Davis 1939, Severaid 1950).

Pygmy rabbits feed primarily on big sagebrush, sometimes even climbing into the tops of the larger plants. They select big sagebrush even when other shrubs are available. In winter, big sagebrush may comprise up to 99% of their diet; grasses (*Agropyron* spp. and *Poa* spp.) may comprise 30-40% of their diet in summer (Bailey 1936, Green 1978, Wilde 1978).

Reproduction

Sexual development in males begins in January, peaks in March and declines in June (Janson 1946, Wilde 1978). Females are fertile from late February through March in Utah (Janson 1946) and from late March through late May in Idaho (Wilde et al. 1976). The gestation period lasts from 26 to 28 days (Bradfield 1975). Litter size ranges from five to eight and averages six (Wilde et al. 1976, Wilde 1978, Davis 1939). Females are able to produce three litters per year (Green 1978, Wilde 1978).

Population Status and Threats to Survival

The status of the pygmy rabbit varies widely, from secure populations in large expanses of sagebrush such as occur in Idaho, to isolated remnants in Washington. Because the rabbit is totally dependent upon big sagebrush, particularly the highest densities, it is quite vulnerable. Wilde (1978) goes so far as to say that pygmy rabbits and humans may be incompatible. Certainly, large areas in the rabbit's range have been permanently converted to other uses such as dryland farming and irrigated cropland. In addition, rangeland is often improved for livestock use by reducing the shrub cover using various methods, all of which render the shrub-steppe

rangeland unsuitable for pygmy rabbits.

The species will not cross even moderately large areas of open ground (Bradfield 1975, Weiss and Verts 1984). Because of this limited immigration, some populations are subject to the principles of island biology. They exist in "islands" of sagebrush inside large areas of altered habitat. While their distribution was at one time continuous, many populations are now isolated. The probability of survival of these populations is related to the size of the contiguous habitat that comprises the "island." Genetic drift and stochastic events can cause spontaneous local extinctions; fire, disease and climatic fluctuations can have major effects. As the size of the "island" is diminished, the likelihood of local extinction increases. This phenomenon is particularly critical on the fringes of the range. One area in Washington has been isolated for over 23 years.

Weiss and Verts (1984) stated that the pygmy rabbit may be subject to rapid population declines in Oregon. They found that ten of the 15 active sites sampled in 1982 showed no evidence of activity one year later. When declines occur in isolated populations, extinctions are likely. These extinctions are cumulative, progressively reducing the extent of the species' range.

In all parts of their range, overgrazing can impact populations. While overgrazing will eventually increase the shrub densities, the immediate impact is to reduce the summer grass and forb forage available to the rabbits. Cattle in particular also damage the structure of the sagebrush, breaking off branches and opening the canopy. If overgrazing occurs in occupied pygmy rabbit habitat for several seasons in succession, particularly if the habitat is limited to begin with, the impact could be extreme. Restocking will occur when overgrazing ceases if other populations occur within contiguous habitats, but not if the area is isolated.

Green and Flinders (1980a) believe that sagebrush growing along riparian areas near streams may provide avenues of dispersion between larger blocks of sagebrush. This could be used as a management tool, protecting or creating such corridors of sagebrush, to assist in the maintenance and mixing of populations.

The pygmy rabbit uses a unique habitat: a combination of dense sagebrush, deep soil suitable for burrowing, and good grass and forb cover. Unfortunately this habitat has been reduced in most areas in the west. However, the fact that this species can use sites which were once disturbed by grazing or cultivation and have reverted to big sagebrush indicates that suitable habitat can be created. Where small populations of pygmy rabbits now exist, steps can be taken to increase the amount of suitable habitat. This may require a commitment of range or agricultural lands to restore significant areas to sagebrush range. Where isolated populations now occur, corridors can be created to connect sites and thereby reduce the chances of local extirpations. In some cases this would only require a change in farming practices, leaving sagebrush along draws and field edges, connecting adjacent areas of sagebrush habitat.

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Chapter 7: The European Rabbit *Oryctolagus cuniculus*

John A. Gibb

Taxonomy

The European rabbit *Oryctolagus cuniculus* (Linnaeus 1758), or cony of our Norman forbears, is the ancestor of all domestic breeds. The genus *Oryctolagus* is monospecific. There are usually considered to be two main subspecies, the now widespread and larger *O. c. cuniculus* (maximum weight about 2kg) from central Europe and the smaller (maximum 1kg) *O. c. huxleyi* from the south of the Iberian peninsula. The validity of *O. c. cnossus* on Crete is dubious. Thompson and Worden (1956) listed six supposed subspecies.

Description

Externally, the European rabbit is distinguished from most of the other five leporids in Europe by its smaller size, relatively shorter ears lacking black tips and the white underside to its tail; also, unlike *Lepus*, young rabbits are usually born underground and are naked, blind and helpless. The European rabbit resembles the American cottontails, *Sylvilagus* spp. and is separated from them on biochemical and behavioral grounds.

As its Latin name implies, the European rabbit is typically a burrowing animal living communally in warrens. These characteristics are not in themselves diagnostic, however. Wild rabbits sometimes live permanently above ground, sheltering by day in dense vegetation, and only breed underground. At low density isolated pairs are not uncommon. This varied lifestyle in different habitats emphasizes the species' marked adaptability.

Distribution

A rabbit resembling the European rabbit was probably present in the pre-Pleistocene fauna of central and western Europe. Apparently it died out in the glacial, except in the Iberian peninsula.

Familiar though the European rabbit may now be, the origin of *O. c. cuniculus* is obscure. Symptomatic of this is that the type locality of *O. c. cuniculus* is in Germany and that of *O. c. huxleyi* in Porto Santo, Madeira, outside their natural ranges. *O. c. cuniculus*, having supposedly arisen in the Iberian peninsula, did not appear in north-central Europe until the Middle Ages. In cataloging the mammals in the British

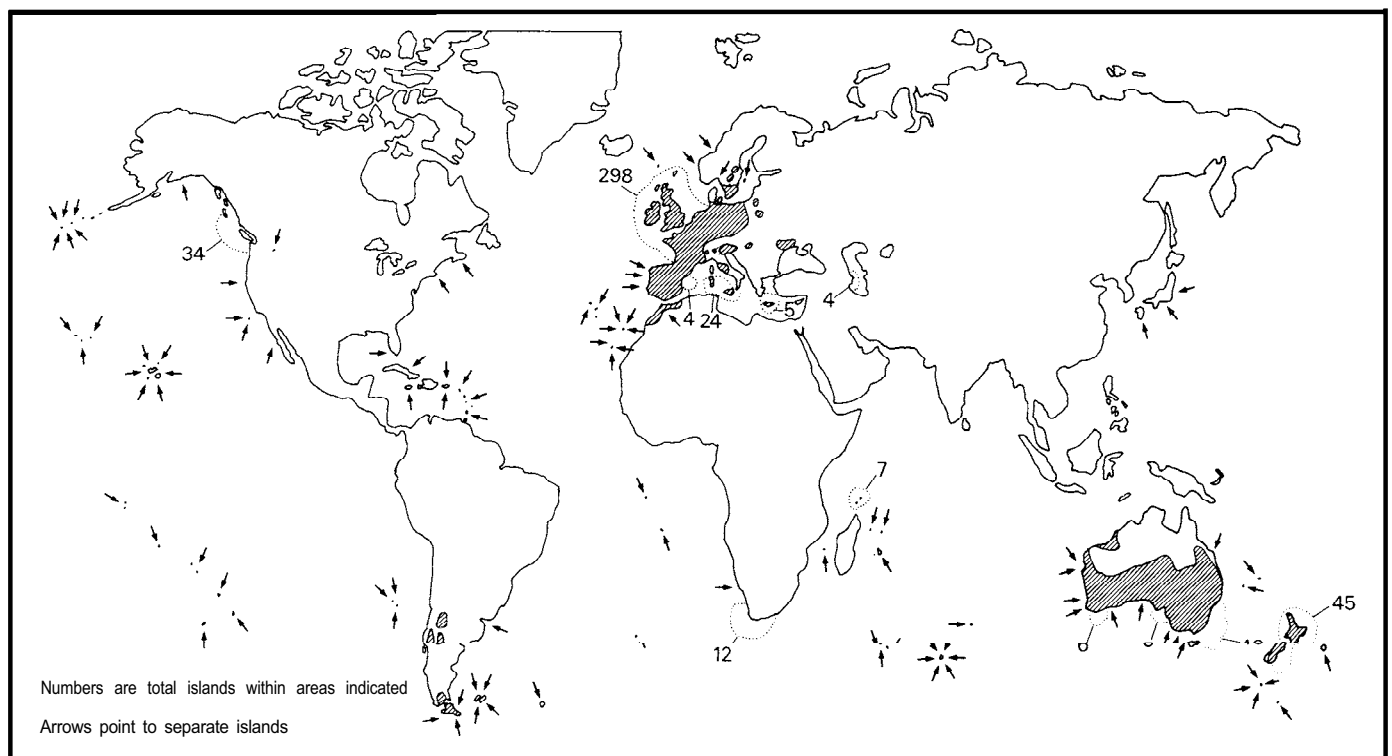


Figure 7.1 Distribution of the European rabbit *Oryctolagus cuniculus*

Museum (Natural History), Miller (1912) listed specimens of *O. c. huxleyi* from Coto Donaña and Seville in southern Spain, near Burgos in north-central Spain, from Nîmes north of the Rhone delta and Digne in the Basses Alpes, 110km north of Toulon, in the south of France. This unbroken arc leaves little room for *O. c. cuniculus* to have evolved within the species' known range.

There is much in favour of Fitter's (1959) suggestion that the Romans produced the larger breed from *O. c. huxleyi* in captivity, and then released it or allowed it to escape into northern France, whence it was later brought to Britain. In which case '*O. c. cuniculus*' may be an impostor and should be known simply as the Feral Rabbit. *O. c. huxleyi* was widely distributed by the Phoenicians on islands off the northwest coast of Africa and in the Mediterranean. Presumably it still exists in the Azores and on Porto Santo and the Salvage Islands of Madeira, and in the Mediterranean on the Balearic Islands, Capri (Italy), Sicily, Sardinia, Tunisia and Crete. Many erstwhile populations of *O. c. huxleyi* on the European mainland have now been replaced by *O. c. cuniculus*, the preferred quarry of hunters because of its larger size.

Though conjectural, Fitter's suggestion draws attention to the uncertain origin of *O. c. cuniculus* and present status and range of *O. c. huxleyi*. Urgent steps are needed to assess the need to protect *O. c. huxleyi*, which may be endangered. As virtually nothing is known of the biology of *O. c. huxleyi*, the following account refers exclusively to *O. c. cuniculus*.

O. c. cuniculus is the larger and perhaps the hardier breed; it has displayed remarkable adaptability to extreme conditions. It survived long sea passages on board sailing ships bound for Australia and New Zealand and to other parts of the globe in the 18th-19th centuries; and on release reached densities unheard of in Europe.

Lever (1985) described the extensive present range of the species with its three foci, in western Europe and North Africa, whence it was shipped to Australia and New Zealand, and to South America. The rabbit's recent crossing of the Andes from Chile into Argentina and spread in Tierra del Fuego is proof that it has not yet been halted. (See Fig. 7.1) .

There are, besides, numerous island populations of the European rabbit around the world; of *O. c. huxleyi* in the eastern Atlantic and Mediterranean, and of *cuniculus* from the Aleutians and islands off Alaska to Phoenix Island almost on the equator in the Pacific, and south to subantarctic Macquarie Island (Flux and Fullagar 1983). The rabbit was a common article of trade among whalers working the southern oceans in the late 18th and early 19th centuries, and was sometimes put ashore on distant islands to supplement stocks of food cached for castaways.

Habitat

Ideal rabbit habitat resembles conditions typical of the Iberian peninsula: a Mediterranean climate with a rainfall of less than about 1,000mm per annum., short herbage and well-

drained, loosely compacted soils that are easily dug, or with secure refuge areas in scrub adjacent to feeding grounds. As Barrett-Hamilton (1910) put it in Britain, "Although it thrives best on dry but rich pastures, the rabbit may be expected wherever a blade of grass can grow, . . .it holds its own in the face of the most relentless persecution... It plants its colonies on almost inaccessible turfey ledges on the sides of sea cliffs and precipices", as well as on the plains. "If it objects to anything it is to cold and wet, but the objection is only relative, since it abounds in the continuous heavy rains of the Mull winters..." as well, one might add, as in the perennially wet climate of sub-antarctic Macquarie Island, a far cry from Mediterranean Spain.

Reproduction

The European rabbit is notoriously prolific. It is liable to breed opportunistically at any season, which contributes to its success as a colonist. In general, in its introduced range, breeding begins and ends earlier in the year the lower the latitude (Gibb et al. 1985). The length of the season, and hence the number of litters produced each year (at the rate of about one per month), depend on the length of the growing season of the herbage on which it feeds. Thus breeding lasts from about four months of the year at higher latitudes to at least nine months in temperate New Zealand. Opportunistic breeding is most marked in semi-arid parts of Australia where droughts lasting many months may be punctuated by occasional heavy rain, to which the vegetation responds vigorously at any season (Wood 1980).

There is a post-partum or seven day oestrous period. Gestation lasts 28-30 days and the young remain in the nest for 20-21 days; they are then weaned. While they are in the nest, the female (doe) visits her young only once a night, for about five minutes.

The female alone builds the nest of dead vegetation lined with fur plucked from her belly. The nest may be placed either in a short offshoot of an established warren or in a separate breeding "stop" about one metre long, so called because the doe stops up the entrance with spoil whenever she leaves. Stops may be dug and stopped days, weeks or even months before they are used; indeed many are never used at all. In Australia, Mykytowycz and Gambale (1965) found that dominant does normally breed in the warrens and subordinate ones (less successfully) in isolated stops. But where there is sufficient scrub cover in New Zealand, rabbits often live permanently above ground and have no warrens, so all breeding is in stops. Elsewhere, extremes of temperature and lack of ground cover may force rabbits to live and breed underground in warrens.

In Wales, Brambell(1944) found occasionally heavy losses and resorption of embryos early in the gestation period. Such losses may be of single embryos or whole litters. The incidence of pre-natal mortality is variable. It is now seen as adaptive in allowing does either to terminate a pregnancy or to



European rabbit *Oryctolagus cuniculus* (Photo by A Apse)

reduce the size of the litter if conditions are unfavourable for lactation, which is the most demanding stage of reproduction (Gibb et al. 1985) .

Litter size at birth peaks in spring when pasture production is maximal. Litters range in size from about three to nine young, with a mean of about four to six in mid-season, falling to three to four during off-peak periods. Winter breeding is normal in Mediterranean climates, where breeding ceases in late spring; but in more temperate climates breeding begins in early spring and continues through to mid-summer. The longest breeding seasons recorded are in warm temperate New Zealand, with a well-distributed rainfall, where more than 50% of the adult females may be pregnant for nine months of the year.

Population Dynamics

Seasonal and regional variation in litter-size is less pronounced than the length of the breeding season; consequently the annual reproductive rate of female rabbits depends pri-

marily on the length of the breeding season. The number of young born per female per year ranges from about 15 to 45, depending on the climate, the latter figure being usual on improved pasture in New Zealand (Gilbert et al. 1987). Male and female rabbits first become fertile when three to four months old, and in New Zealand females of nine to twelve months old breed at the maximum rate (Gibb et al. 1985). If the population is stable, the high reproductive rate must be balanced by a correspondingly high rate of juvenile mortality. It is estimated in Australia that more than 80% of the young born may be killed by predators (mainly foxes and feral cats) either in the nest or within two weeks of leaving it (Wood 1980); others may die later of coccidiosis. This pattern is probably repeated in New Zealand, except that mortality rates must be even higher because reproductive rates are higher, and perhaps also in Spain where predation is certainly heavy. Annual mortality rates of adults more than six months old usually exceed 60% (Gilbert et al. 1987); but may be as low as 25% in low-density populations in New Zealand (Gibb unpubl.). In the wild, rabbits seldom live for more than seven to eight years.

The density of rabbits is of course ultimately limited by plant production. In practice, however, heavy predation commonly prevents numbers building up to the carrying capacity of the land. Populations of rabbits are capable of sustaining massive predation pressures because of their high reproductive rates. In Spain, for instance, the rabbit is an important prey of 19 species of birds of prey and ten mammalian carnivores (Delibes and Hiraldo 1981). There are rather fewer species of predators on rabbits in Australia and Chile, and fewer still in New Zealand. Even so, in New Zealand as in Spain, predation is regarded as the principal cause of death among both young and old rabbits.

Since many predators concentrate on young rabbits, their abundance and effectiveness in limiting rabbit numbers may depend on the length of the rabbits' breeding season coupled with the availability or otherwise of alternative prey for when there are no young rabbits. The effectiveness of predation may thus be curtailed in ecosystems lacking a full complement of predators (as on small islands) or without alternative prey. Climatic extremes, too, may prevent the survival of balanced populations of predators and their prey, as in semi-arid regions of Australia. Predation may also be restricted, as in parts of Britain, where strict gamekeeping almost eliminates predatory 'vermin.' Elsewhere, however, in more varied ecosystems, stable populations of rabbits may persist indefinitely at low to medium density.

Behavior

Rabbits are strongly territorial and form social groups with a strict linear hierarchy of dominance. The dominant male (buck) serves several does, while some younger, subordinate bucks may live peripherally to the group and delay achieving a degree of dominance until they get older. At high density social groups may defend group territories, but at low density rabbits frequently live in small groups of two or three animals or even solitarily (males only?). Neighbouring groups may coalesce and feed together at night, or be joined by bucks visiting from other groups.

Defended territories are usually small, often less than one hectare; but if food is short or distributed unevenly, rabbits may feed communally at night at distances of up to at least 500m away from where they spend the day. Adult rabbits seldom shift their ground permanently, though their territories may "creep" over time. Juveniles sometimes disperse several kilometers from where they were born, though the majority stay put. When introduced to Australia, rabbits spread over unoccupied territory at rates of up to 300km a year, apparently unaided (Myers et al. in press), compared with about 15km a year in New Zealand.

By itself, the territorial behavior of rabbits is incapable of limiting population density, but it may play a part in regulating local densities once numbers have been reduced to a low level by some other means, such as predation (Gibb and Williams in press).

Disease

The advent of myxomatosis from South America, where the *Myxoma* virus is endemic and benign in local *Sylvilagus* sp., to Europe and Australia in 1950-1953 resulted in a tremendous reduction in the numbers of rabbits; more than 99% of some populations succumbed in the early years. The virus is spread mechanically from rabbit to rabbit via the mouthparts of biting insects, notably the rabbit flea *Spilopsyllus cuniculi* and various species of mosquitoes. The absence of the flea and a lack of indigenous vectors prevented the virus from becoming established in New Zealand when it was deliberately introduced in the early 1950s (Filmer 1953); and the absence of vectors was also blamed for its failure in Tierra del Fuego. The introduction of the rabbit flea to Australia in the 1970s, to augment mosquitoes as vectors, has had inconclusive results.

Neither the flea nor the virus has been introduced to New Zealand since the virus first failed to become established, despite vocal pressure by farmers in rabbit-infested districts. Over most of New Zealand rabbits have now been severely reduced in numbers by poisoning with sodium monofluoroacetate (compound '1080') in carrot bait dropped from the air. This has been followed by improved farming practices which encourage natural predation, with the result that most populations are now naturally controlled at low density (Gibb and Williams in press).

In Europe and Australia the more virulent strains of the *Myxoma* virus have gradually been superseded by less virulent strains; and the rabbits themselves have developed a degree of genetic resistance to the virus. As a result, the long-term effectiveness of myxomatosis in limiting rabbit numbers is in question, and in recent years they have staged a considerable resurgence in both Britain and Australia. Sporting interests in France and Italy have been responsible for the introduction there from America of the eastern cottontail *Sylvilagus floridanus*, which is resistant to myxomatosis, to substitute for the diminished supply of *Oryctolagus*. The wisdom of this action is dubious, to say the least.

Another lethal viral disease of rabbits is being reported at the time of writing. The type of virus involved is still uncertain. Apparently the first outbreak occurred in 1984 in a consignment of angora rabbits from West Germany to China. Provisionally known as viral haemorrhagic disease (VHD), it has been linked with a current viral disease of hares (*Lepus europaeus*) in Europe, which has reduced many wild populations. It is not known whether hares or other genera of rabbits are susceptible to VHD, or whether it is likely to spread to other countries with wild *Oryctolagus*. VHD is apparently spread by aerosol infection so, unlike myxomatosis, it needs no intermediate vector.

Since 1984, VHD is reported to have killed millions of domestic rabbits in Italy and outbreaks have been reported among wild rabbits in at least three separate localities in Spain. Fear of the disease spreading has stopped the export of live rabbits from Spain to restock hunting reserves in France. Until recently some 100,000 live rabbits have been exported

annually to France and French hunters are now reported to have been inquiring about importing wild rabbits from Western Australia instead!

Initially heavy mortality (>90%) has been reported among adult wild rabbits when first confronted with VHD in Spain. Young rabbits less than about eight weeks of age may have become infected with VHD, but they develop immunity to it and are not killed. This may limit its effectiveness as a self-perpetuating means of controlling wild rabbits.

Research on VHD can only be undertaken in specially equipped laboratories as at Pirbright in England and Geelong in South Australia. Research is obviously needed to identify the virus and to predict its impact on wild populations.

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Chapter 8: The African Rabbits

A.G. Duthie and T.J. Robinson

Species

Riverine rabbit *Bunolagus monticularis* (Thomas 1903), Bunyoro rabbit *Poelagus marjorita* (St. Leger 1932), greater red rockhare *Pronolagus crassicaudatus* (I. Geoffroy 1892), Jameson's red rockhare *Pronolagus randensis* (Jameson 1907), Smith's red rockhare *Pronolagus rupestris* (A. Smith 1834)

Status and Summary

Several problems exist in determining the status of the African rabbit species presented in this chapter. In general terms, their small body size, nocturnal habits and low conservation priority, exacerbated by the third world setting, have all contributed in various degrees to the paucity of biological data. Unlike Europe and North America, where lagomorphs are important game species and have consequently attracted the attention of biologists, leporids have traditionally been regarded of little consequence in Africa, an attitude that has, until recently, pervaded both professional and lay circles. A notable exception concerns the riverine rabbit *Bunolagus monticularis* where conservation efforts by the Wildlife Society of Southern Africa and South African Nature Foundation, in concert with research endeavors, have done much to draw attention to the plight of the species. Consequently, the data on the riverine rabbit are more comprehensive than those on the Bunyoro rabbit *Poelagus marjorita* and the three species of rockhares *Pronolagus* which, in turn, is reflected in the accounts of the taxa and in information on basic biology and distribution patterns.

In particular, the current status of the Bunyoro rabbit *Poelagus marjorita* is enigmatic. Much of the species' historic range is in areas which have been subjected to prolonged civil strife. Nonetheless, all reports seem to indicate that the species is locally abundant. It should be cautioned, however, that only the most rudimentary of data are available, and our treatment of this species as not threatened is permitted more by ignorance than sound science and should be considered tentative pending future study.

Regional considerations were not considered important in setting conservation priorities for the African lagomorphs since particular taxa may, by virtue of limited distribution, be rare in one country but relatively abundant in another. We realize, however, that this view is flawed in respect of taxa with disjunct distribution patterns, perhaps most pronounced in the monotypic Bunyoro rabbit and also Smith's red rockhare *Pronolagus rupestris* and Jameson's red rockhare *P. randensis*,

and those for which comprehensive taxonomic data on the species are unavailable. The problems of cryptic species and the conservation of geographic genetic variation are of profound importance in the development of long term conservation strategies, but cannot be sensibly addressed with the existing data.

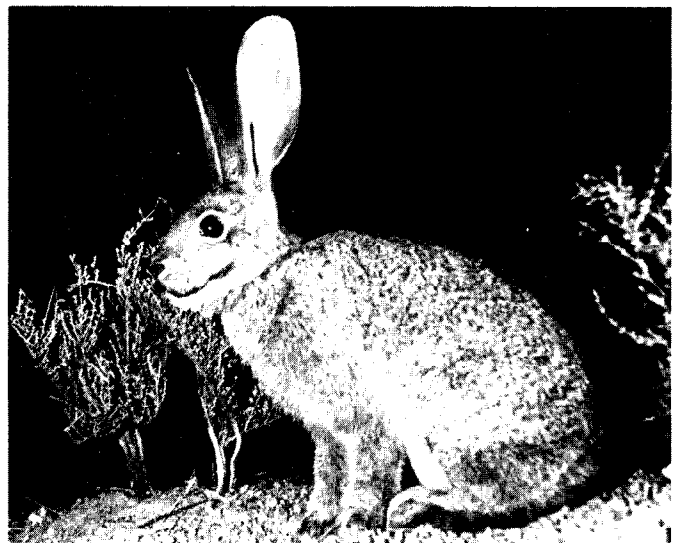
Finally, the species covered by this report are restricted to two geographic regions, the Southern African Subregion and the Central African Moist Savanna. The former may be regarded as particularly pertinent in future conservation strategies aimed at maintaining species diversity, characterized as it is, by both a high level of species endemism and a rich leporid fauna.

Species Accounts

The Riverine Rabbit *Bunolagus monticularis*

Taxonomy and Description

Originally described as *Lepus monticularis* Thomas (1903), it was separated generically some years later by Thomas (1929). Although the riverine rabbit superficially resembles the Cape hare *L. capensis*, in external and cranial morphology (Robinson and Dippenaar 1987; head body length 430mm; tail 92mm; hindfoot length 104mm and ear length 116mm) it nonetheless has several features which distinguish it at both generic (Robinson and Skinner 1983, Corbet 1983) and spe-



Riverine rabbit *Bunolagus monticularis*
(Photo by T. J. Robinson)

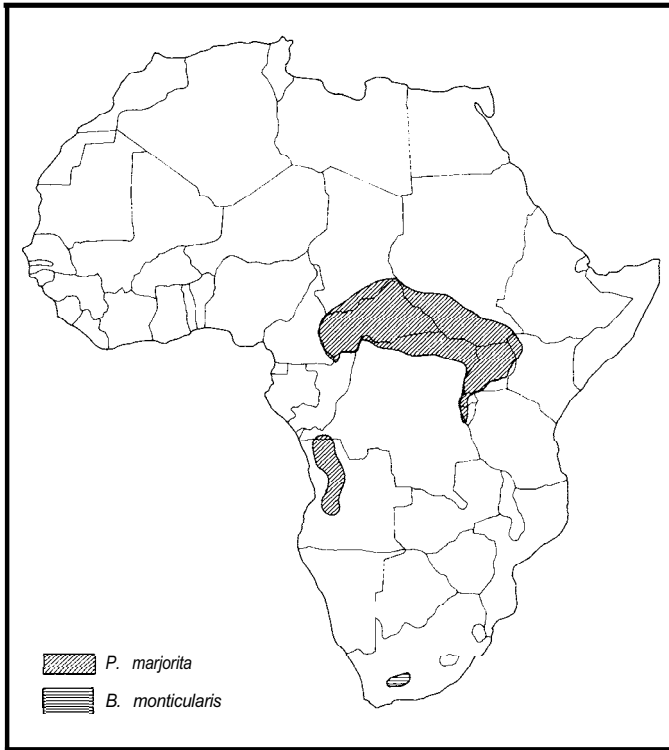


Figure 8.1. Distributions of riverine rabbit *B. monticularis* and Bunyoro rabbit *Poelagus marjorita* in Africa.

cies level (Robinson 1982, Robinson and Dippenaar 1987). A characteristic feature of the taxon, not shared by other members of the family in the Southern African subregion, is the dark brown stripe running along the lower margins of the jaw towards the base of the ear. Distinguishing external markings which unambiguously separate it from the Cape hare and the rockhare species are, respectively, a uniformly brown-colored tail (black and white in the Cape hare) and long ears (63-106mm in the rockhare species). No subspecies have been described.

Distribution

The species is limited to the Southern African subregion and, more specifically, is endemic to the central Karoo (31°22'S, 22°E) of South Africa's Cape Province (Fig. 8.1). Recent surveys (Duthie *et al.* 1989) suggest it survives only in the dense, discontinuous karoid vegetation in the districts of Victoria West, Beaufort West and Frazerburg, an area of approximately 86km² which is linearly distributed along the seasonal rivers in these regions. In historic times the species' range was known to include the riverine vegetation in the districts of Sutherland and Calvinia (approximately 136km²) but recent extensive surveys suggest that it has disappeared from this area (Robinson 1981, Duthie *et al.* 1989).

Habitat and Ecology

The riverine rabbit inhabits dense riparian growth along the seasonal rivers in the central Karoo. Vegetation analyses of

the typical habitat, designed to determine the percentage vegetation cover, percentage occurrence and mean plant height and width, indicate that *Salsola glabrescens* (34.8%) and *Lycium* species (11.2%) predominate, while *Pteronia eythrocaetha* (7.9%), *Osteospermum spinescens* (5.3%), *Kochiapubescens* (6.5%) and *Galenia procumbens* (4%) contribute significantly (Duthie *et al.* 1989). This investigation also revealed that grasses are poorly represented, their cover being approximately one fifth that of dicotyledons. Noteworthy from the investigation was the observation that almost 68% of the remaining riverine rabbit vegetation is found to be associated with an interconnected network of rivers; principally the Sak, Klein Sak and Riet, Klein Riet in the central Karoo.

The monotypic riverine rabbit is solitary, has a polygamous mating system and is nocturnal in habit. During daylight hours it makes use of forms usually sited at the base of overhanging vegetation. Home ranges are intrasexually exclusive with those of the male (20.9ha ± 2.9) overlapping those of the female (12.9ha ± 5.6; Duthie 1989).

Analysis of faecal samples collected in the field from areas previously determined as being inhabited only by riverine rabbits, indicates that the species is predominantly a browser. Flowers and leaves of the dicotyledonous *Pteronia eythrocaetha*, *Kochiapubescens*, *Salsola glabrescens*, *Rosenia humilis* as well as representatives of the Mesembryanthemaceae are most commonly eaten. Grasses are included in the diet when these are available in the wet season (Duthie 1989).

The African wild cat *Felis libyca* is a predator of the species (Duthie 1989).

Reproduction

Although data on reproduction are fragmentary, several generalizations can be made. First, one, possibly two young are born to reproductively-active females in the period August through May. Limited observations of captive animals suggest the existence of post partum oestrus and breeding synchrony in the species. The young weigh approximately 40g at birth and are born in a fur and grass lined breeding stop similar in construction to that reported for the European rabbit *Oryctolagus cuniculus* (Lloyd and McCowan 1968) and the New England cottontail *Sylvilagus transitionalis* (Tefft and Chapman 1987). The burrow has an entrance 90-105mm wide, is approximately 200-300mm long and widens into a chamber 120-170mm broad. Interestingly, the burrow opening is plugged with soil and twigs when the stop is not in use (Duthie 1989). The youngest juveniles noted in the wild weighed 500-600g, possibly indicating that they remain in the breeding stop for relatively long periods prior to leaving to forage independently.

Population Status and Threats

Two censuses conducted in discrete sections of the typical habitat have yielded densities of 0.064 and 0.166 riverine rabbits per hectare (Duthie 1989). Extrapolation of these values to remaining habitat indicates that this vegetation



Habitat of the riverine rabbit *Bunolagus monticularis*
(Photo by T. J. Robinson)

could possibly support a total population of approximately 1,500 rabbits. That this figure may, however, represent an overestimation is suggested by the observation that, in spite of intensive surveys, no evidence of species occurrence was noted for the Ongers river which alone supports approximately 21% of remaining suitable habitat.

Several reports have drawn attention to the destruction of the riverine vegetation in this region as a possible reason for the species' disappearance from large tracts of its former range (Robinson 1981) but the extent of the destruction was not quantified. A recent approximation, calculated from 1:50,000 aerial photographs of the central Karoo, indicates that upwards of 60% of the original riparian vegetation has been destroyed through cultivation (Duthie et al. 1989). The destruction has been attributed to a now largely defunct scheme to cultivate wheat on the banks of these rivers which, by 1950, had failed due to lack of irrigation water (Green 1955).

While the extent of vegetation destruction is significant it is currently static. New cultivation still occurs adjacent to farmsteads, but this is limited in extent and does not, at present, represent any significant threat to the remaining habitat. This said, however, the spectre of extinction for this species is very real. Even preserving the remaining habitat may be insufficient to ensure the long-term conservation of the species, since the population numbers are so low and the distribution appears fragmented along the rivers. This will tend to make the isolates more susceptible to local extinctions as well as contributing to the possible disruption of gene flow between adjacent subpopulations.

Conservation Measures Proposed and Adopted

The riverine rabbit is currently listed as endangered in both the IUCN and South African Red Data books. It is also protected by a Cape Provincial Nature Conservation Ordinance which prohibits its hunting or capture.

A captive breeding colony has been successfully established at the De Wildt Cheetah Research Center (24°50'S, 26°54'E). Surplus specimens from this colony will be used for

relocation to suitable areas within its historic distribution. No national reserve has yet been proclaimed for the species, but recent additions to the Karoo National Park (32°12'S, 22°16'E) may prove suitable for relocation of the species once the vegetation has recovered from the effects of overgrazing.

Steps have been taken to have the farm which has formed the focus of research on the species (Duthie 1989) proclaimed a conservancy under South Africa's Natural Heritage Programme. The site (31°21'S, 22°38'E) is situated along the Klein Brak River near the town of Victoria West. A riverine rabbit awareness programme among the farmers of the central Karoo has been instituted.

Conclusion

The monotypic riverine rabbit is the only species of lagomorph on the African continent regarded as endangered. This rating is based on the degree of threat to the population, which is exacerbated by its extremely small numbers and habitat specificity (Duthie et al. 1989), as well as on its taxonomic uniqueness (Robinson and Skinner 1983).

Bunyoro Rabbit *Poelagus marjorita*

Subspecies: *Poelagus marjorita larkeni* (St. Leger 1935), *Poelagus marjorita marjorita* (St. Leger 1932), *Poelagus marjorita oweni* Setzer 1956

Taxonomy and Description

Originally described as *Lepus majorita*, the species was later elevated to full generic rank (see Honacki et al. 1982). Subsequently, it was included as a subgenus of the rockhares *Pronolagus* (Ellerman and Morrison-Scott 1951) and a species of *Caprolagus* (Gureev 1964 in Corbet 1983). *Poelagus marjorita* is currently regarded as a monotypic genus (Petter 1972) for which the above three subspecies have been described. However, we are unaware of any recent rigorous taxonomic investigation of the species. Given the extensive range and apparent geographic isolation of the Angolan population, a taxonomic study should be encouraged.

The genus appears to lack diagnostic cranial features (Corbet 1983). The tail is reported to be brownish yellow dorsally and white ventrally; the ears and hindlegs are short and the pelage harsher than other African leporids (Walker 1964). Head and body length is given as 440-500mm, tail length as 45-50mm, hindfoot 90-100mm, ear length 60-65mm and the species weighs approximately 2-3kg (Kingdon 1974).

Distribution

Kingdon (1974) reports the distribution to extend from southern Chad eastwards through southern Sudan, northeastern Zaire, northwestern Kenya and southwards to the northern tip of Lake Tanganyika. If the current distribution maps are accurate and do not reflect a sampling hiatus, an isolated population would appear to exist in Angola, with a distribu-

tion extending from west-central Angola northwards into southern Zaire (Fig. 8.1).

Habitat and Ecology

The Bunyoro rabbit is a species of moist savanna found in grasslands and *Isoberlina* woodlands in association with rocky outcrops and, to a lesser degree, with forest (Verheyen and Verschuren 1966, Kingdon 1974). They are frequently found together with the rock hyrax, possibly sharing rock crevices with the latter, and in the western Rift valley occupy habitat similar to that of the rockhares (Kingdon 1974).

Bunyoro rabbits feed nocturnally in groups which consist of pairs, or females accompanied by young (Kingdon 1974). During daylight hours they lie up solitarily in forms made in thick vegetation.

The species is reported to forage on flowers and sprouting grasses and is much attracted to heavily grazed, newly mowed or burnt areas where the grass is short (Kingdon 1974). Leaves of peanut and rice plants are taken in the areas where cultivation fringes suitable habitat (Akaibe pers. comm.).

As with all lagomorphs, this species is probably taken by all opportunistic raptors and carnivores. Major predators would include *Felis serval*, *Genetta tigrina* and *G. servalina*, as well as hawks and owls (Kingdon 1974).

Reproduction

Verheyen and Verschuren (1966) and Kingdon (1974) recorded juveniles and pregnant or lactating females in all months, suggesting that breeding occurs throughout the year. Their gestation is thought to be about five weeks (Kingdon 1974). One or two altricial young are born in breeding stops, the entrance of which is concealed with grass and soil (Walker 1964, Kingdon 1974).

Population Status and Threat

The species is common and well protected in the Garamba National Park in northeastern Zaire (Verheyen and Verschuren 1966) and is also reasonably abundant in southern Sudan (Kingdon pers. comm.). The status in other areas, particularly Uganda, Chad and Angola are unknown. Akaibe (pers. comm.) reports that the species' savanna habitat is ploughed under to a limited extent to provide for the cultivation of peanuts and rice and that it is also frequently hunted using nets and dogs. Kingdon (1974) also reports that the species habitat is burnt annually, sometimes biennially, removing the grassland habitat and leaving the species more vulnerable. The extent of this threat is unknown.

Conservation Measures Proposed and Adopted

As far as we have been able to ascertain, the species is not afforded any form of legislative protection. It is, however, reported to be locally abundant, and occurs in the Garamba National Park and Murchison Falls National Park. Possibly no form of protection may be required.

Conclusion

Although data on the distribution of the Bunyoro rabbit are sparse and estimates of population densities unavailable, all indications are that the species is not under threat.

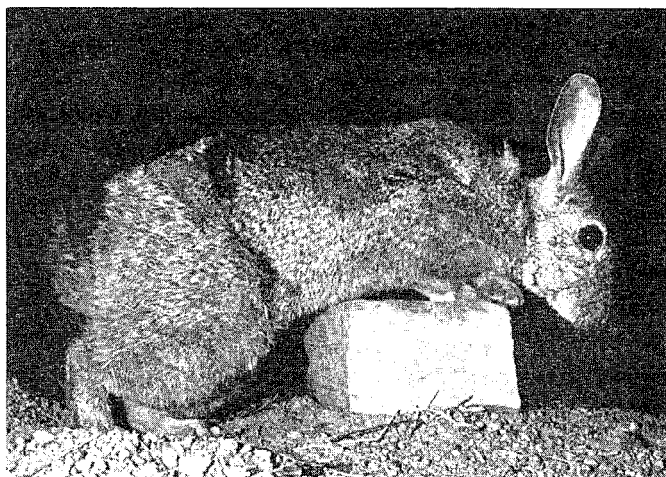
The Rockhares *Pronolagus* Lyon 1904

Species: Greater red rockhare *Pronolagus crassicaudatus* (I. Geoffroy 1892), Jameson's red rockhare *Pronolagus randensis* (Jameson 1907), Smith's red rockhare *Pronolagus rupestris* (A. Smith 1834)

Excluding taxonomic and distributional data, little biological information is available for the three species.

Taxonomy and Description

The type specimen was originally described as *Lepus crassicaudatus* I. Geoffroy but was corrected to *Pronolagus crassicaudatus* by Lyon (Lyon 1906 in Meester et al. 1986). The rockhares have been subjected to a variety of taxonomic interpretations with one to six species being recognized (Roberts 1951, Peddie 1975). As is currently understood, however, the genus comprises three distinct species: Smith's red rockhare *P. rupestris*, Jameson's red rockhare *P. randensis* and the greater red rockhare *P. crassicaudatus* (Robinson and Dippenaar 1983, Meester et al. 1986 amongst others). Lundholm (1955) regards *randensis* as a synonym of *crassicaudatus*. A combination of external features, including the tail which is uniformly reddish brown, brown or dark brown and the short ears (63-109mm) provide a ready means of distinguishing representatives of the genus from other Southern African leporids (Robinson 1982). Distinctive, yet subtle, pelage dif-



Jameson's red rockhare *Pronolagus randensis*
(Photo by T. J. Robinson)

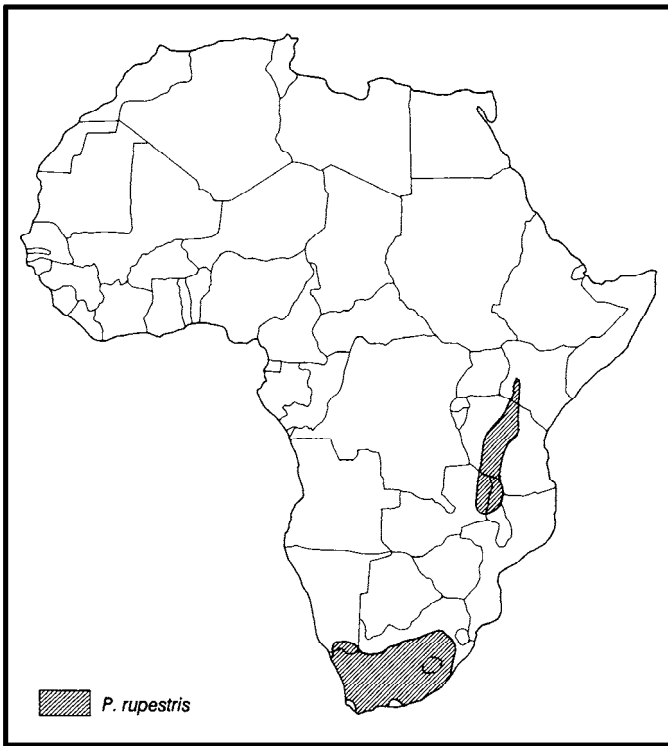


Figure 8.2 Distribution of Smith's red **rockhare** *Pronolagus rupestris* in Africa

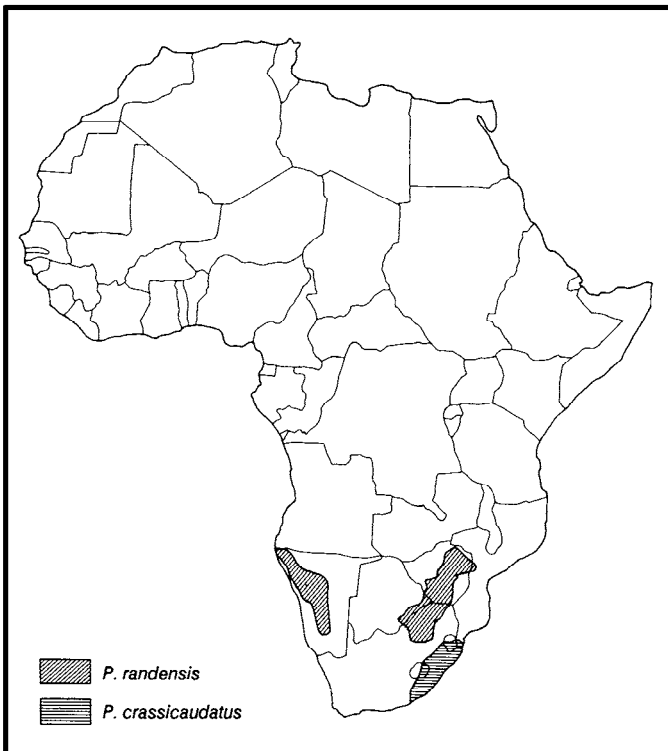


Figure 8.3 Distribution of the greater red **rockhare** *Pronolagus crassicaudatus* and Jameson's red **rockhare** *P. randensis* in Africa

ferences and differences in the shape and size of the crania are useful in distinguishing the three species (Robinson 1982).

The taxonomy of the subspecies remains uncertain. Petter (1972) lists ten subspecies of Smith's red **rockhare** *P. rupestris*, but Meester et al. (1986), following Shortridge (1934), consider *australis* to include *mulleri*, and *whitei* to be a subspecies of *P. randensis*. In summary therefore, the following subspecies are recognized: In southern Africa *P. r. rupestris* (A. Smith, 1934); *P. r. melanurus* (Ruppell, 1842); *P. r. curryi* (Thomas, 1902); *P. r. saundersiae* (Hewitt, 1927); *P. r. australis* Roberts, 1933; *P. r. fitzsimonsi* Roberts, 1938 and *P. r. barretti* Roberts, 1949. Outside southern Africa, two subspecies are accepted: *P. r. nyikae* (Thomas, 1902 - eastern Zambia and northern Malawi) and *P. r. vallicola* Kershaw, 1924 (Rift Valley, Kenya and possibly northern Tanzania).

Following Ellerman et al. (1953), Petter (1972) and Meester et al. (1986) five subspecies of the greater red **rockhare** *P. crassicaudatus* are recognized, although neither their status nor the geographic limits are well defined. Smithers (1983) feels that *P. c. bowkeri* Hewitt, 1927 may be a subspecies of *P. rupestris* and that the status of *P. c. kariegae* Hewitt, 1927 is uncertain. However, by consensus, the five subspecies are: *P. c. crassicaudatus* (I. Geoffroy, 1832); *P. c. ruddi* Thomas and Schwann, 1905; *P. c. kariegae* Hewitt, 1927; *P. c. bowkeri* Hewitt, 1927 and *P. c. lebombo* Roberts, 1936.

Finally, ten subspecies of Jameson's red **rockhare** *P. randensis* are recognized by Petter (1972) although Meester et al. (1986) have provisionally listed only nine, regarding *fitzsimonsi* as a subspecies of *rupestris*; and *whitei*, which is included in *P. rupestris* by Petter (1972 - see above) is thought to have priority over *ekmani* (Meester et al. 1986). Interestingly, Meester et al. (1986) speculate that there may in fact only be an eastern (*P. r. randensis*) and western (*P. r. caucinus*) subspecies. Nonetheless, pending further study the nine subspecies provisionally recognized by these authors are: *P. r. randensis* Jameson, 1907; *P. r. powelli* Roberts, 1924; *P. r. makapani* Roberts, 1924; *P. r. capricornis* Roberts, 1926; *P. r. caucinus* Thomas, 1929; *P. r. kobosensis* Roberts, 1938; *P. randensis whitei* Roberts, 1938; *P. r. kaokoensis* Roberts, 1946 and *P. r. waterbergensis* Hoesch and Von Lehmann, 1956.

Distribution of Smith's red **rockhare**

The species is widely distributed in the Southern African subregion, occurring throughout South Africa's Cape Province except for the coastal forests and the extreme northern reaches of the Province. It is found in the Transkei, southern and central Natal, the Orange Free State, southeastern Transvaal and the western fringes of the Namibian escarpment. Importantly, it occurs extraliminally in Malawi, eastern Zambia, central Tanzania and southwestern Kenya (Fig. 8.2; Meester et al. 1986).

Distribution of Greater red **rockhare**

The species appears to be endemic to the Southern African subregion and, in particular, the eastern Cape Province, Transkei, Natal, eastern Lesotho, Swaziland, southeastern

Transvaal and southern Mozambique (Fig. 8.3; Meester et al. 1986).

Distribution of Jameson's red rockhare

The species is characterized by a disjunct distribution and is largely endemic to the Southern African subregion. Meester et al. (1986) report that an eastern population extends from the Vaal River near Parys, through the central, northern and western Transvaal, southern, eastern, northeastern and western Zambia, western Mozambique and southeastern Botswana. Similarly, a western population is thought to extend northwards from Rehoboth along the escarpment to southwestern Angola (Fig. 8.3).

Habitat and Ecology

All rockhare species are restricted to rocky situations in association with grass or scrub on hill and mountainsides, irrespective of whether these are basalt, granite or sandstone formations (Smithers 1983). In an ecological study on Jameson's red rockhare, Peddie (1975) recorded the species to rarely venture any significant distance from its rocky habitat. The greater red rockhare is reported to occupy suitable habitat from sea level to elevations of 1,550m.

The confinement of rockhares to this characteristic habitat is noteworthy, since distribution is discontinuous and there are extensive tracts of intervening country which is unsuitable. This creates a patchwork distribution of habitat "islands" which may be of considerable importance in determining geographic variation and in the planning of genetic conservation strategies for the respective taxa.

When lying up, rockhares appear to be gregarious although this is probably more as a result of occupying restricted areas of rocky habitat (Rautenbach 1982; Smithers 1983; Peddie 1975). All species forage individually at night but spend daylight resting in rock crevices or in forms. Evidence of the taxon's solitary nature is provided by Peddie (1975) who found only 15% of the nocturnal sightings of Jameson's red rockhare in the Zimbabwean Matopos to be of pairs. Smithers (1983) notes that the female rock rabbit may be accompanied by more than one male during the breeding season.

Rockhares have been reported to be the most vocal of the African lagomorphs. Roberts (1951) describes them as uttering loud startling screams when disturbed at night although this behavior has never been noted by either corresponding author. Other vocalizations include a churring sound in a hand caught juvenile, and an adult disturbed before sunrise "barked" before fleeing (Duthie pers. obs.).

All three rockhare species deposit their characteristics disc-like faeces in middens which may serve a social function (Smithers 1983).

All species are grazers (Smithers 1983). More than 90% of identifiable plant remains in the faeces of a single Smith's red rockhare analyzed by Stewart (1971) were of monocotyledonous origin. Jameson's red rockhare prefers feeding in areas of sprouting grass and avoids areas of dense aerial cover and moribund vegetation (Peddie 1975) an observation which

holds for the other taxa as well.

Leopards *Pantherapardus*, Cape eagle owls *Bubo capensis* and black eagles *Aquila verreauxi* are known to take rockhares (Peddie 1975).

Reproduction

Available evidence suggests that Jameson's red rockhare breeds throughout the year (Peddie 1975). No comparable data exists for the other two species. Both Jameson's red rockhare and Smith's red rockhare have one or two young per litter (Peddie 1975; Shortridge 1934; Smithers and Wilson 1979; Rautenbach 1982). Altricial Smith's red rockhare young are born in nests constructed of plant debris which are lined with fur (Shortridge 1934; Pepler pers. comm.). Further support for an altricial birth is provided by the study of near-term fetuses which are very sparsely haired (Smithers 1983).

Population Status and Threat

The ranges of all three species are well represented in National and Provincial Parks and Wildlife refuges in Southern Africa and none of the species are considered to be in any danger. As stated previously however, the disjunct distribution and probable genetic heterogeneity between populations are important conservation considerations but, with available data, this cannot be addressed. While the northernmost population of Smith's red rockhare is widespread in southwestern Kenya and central Tanzania, it is presumably a relict of a once continuous distribution; its precise relationship to the more southern population needs clarification. Likewise, a similar situation holds for the two geographic populations currently recognized as belonging to Jameson's red rockhare (Fig. 8.3).

Conservation Measures Proposed and Adopted

The representative species are locally abundant and well represented in National and Provincial parks in South Africa, as well as in similar facilities in other regions of their respective geographic ranges. The various rockhare species are afforded seasonal protection as game species by Provincial Nature Conservation Agencies.

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Chapter 9: The Hispid Hare *Caprolagus hispidus*

D.J. Bell, W.L.R. Oliver and R.K. Ghose

Status and Summary

The hispid hare *Caprolagus hispidus* (Pearson 1839) is Endangered. It still exists in a few isolated pockets across the former range of its tall grassland habitat in northern India and southern Nepal. It is threatened by habitat destruction for agriculture, forestry, human settlement, flood control and irrigation schemes, together with the adverse effects of dry season burning, overgrazing and harvesting of remaining tall grasslands.

Physical Characteristics

The mean (and range of) body weights recorded from the four sexually mature male and three female hispids by Bell (1987) was 2,248g (1,810-2,610g) and 2,518g (1,885-3,210g) respectively (the 3,210g female was heavily pregnant).

The coarse, bristly coat is dark brown on the dorsal surface, due to a mixture of black and brown hairs, ventrally brown on the chest and whitish on the abdomen. In contrast to the longer ears and white underside to the tail found in the sympatric Indian hare *Lepus nigricollis ruficaudatus*, the short (adult length approx. 30mm) tail is brown throughout in the hispid hare and the ears shorter (adult length approx. 56mm) (Bell 1987).

Distribution

Historically recorded in tracts along the southern Himalayan foothills from Uttar Pradesh through Nepal and West Bengal to Assam, extending southwards as far as Dacca in Bangladesh, although fossil evidence suggests a more extensive Pleistocene distribution which included central Java (Blandford 1888, Dawson 1971). Later specimens were recorded from the North Kheri, Uttar Pradesh/Nepal border in 1951; from Chuka Dhaya, Pilibhit Forest Division, Uttar Pradesh in 1960; the Goalpara District of southwest Assam and the Rajagarh areas of the Mangaldai sub-division of Darrang District of northwest Assam in 1971 (IUCN 1974) (See Table 9.1 and Fig. 9.1). The latter specimen (hailed by several authors as the rediscovery of the species) was collected from the vicinity of the Barnadi Reserve Forest near Rajagarh Village. It was taken to the Attareekhat Tea Estate, where it was kept alive for approximately one month (Mallinson 1971, Tessier-Yandell 1972). Several specimens were subsequently reported or collected in areas due east and west of Barnadi: namely in

Manas Reserve Forest, Manas Sanctuary and Khalingdaur Reserve Forest (Oliver 1979a, 1980). The Khalingdaur population was almost certainly exterminated by the mid-1970's as a result of extensive burning and reforestation, while another from the Gohpur Reserve Forest is also reported to have been exterminated as a result of the complete swamping of that area by illegal immigrants in 1979 (Oliver 1981).

The species has been reported on many occasions in the Manas Tiger Reserve and adjacent Reserve Forests. Specimens from this area were collected for the Assam State Zoo, Gauhati but none of these animals survived very long.

A field survey of Sanctuaries and Reserve Forests in northwest Assam, conducted by Oliver in 1977, included the capture of a live specimen in Barnadi Reserve Forest, Darrang District, while long-netting for the closely-associated pigmy hog *Sus salvanius*. The three other areas in Assam where the hispid hare has recently been reported are Ripu Reserve Forest, Kochugaon District (west of Manas) (Paramenda Lahan, pers. comm.), Subankhata Reserve Forest (Deb Roy pers. comm.) and the Orang Wildlife Sanctuary, Darrang District (P.C. Das, pers. comm., Oliver 1984).

More recently, the species has also been reported in a number of areas outside Assam. These areas are: the Jaldapara Wildlife Sanctuary (Oliver 1984, Ghose and Ghose 1984) and Buxa Tiger Reserve (Oliver 1984) in northwest Bengal; Valmiki Wildlife Sanctuary, West Champaran District, N.W. Bihar (Ghose in press); Kanha National Park, Madhya Pradesh (Bell and Oliver in prep.); Dudwa National Park in the Kheri District of Uttar Pradesh and Royal Chita-



Male hispid hare fitted with radio-collar. Note the large nasal bone and short ears (Photo by Diana Bell)

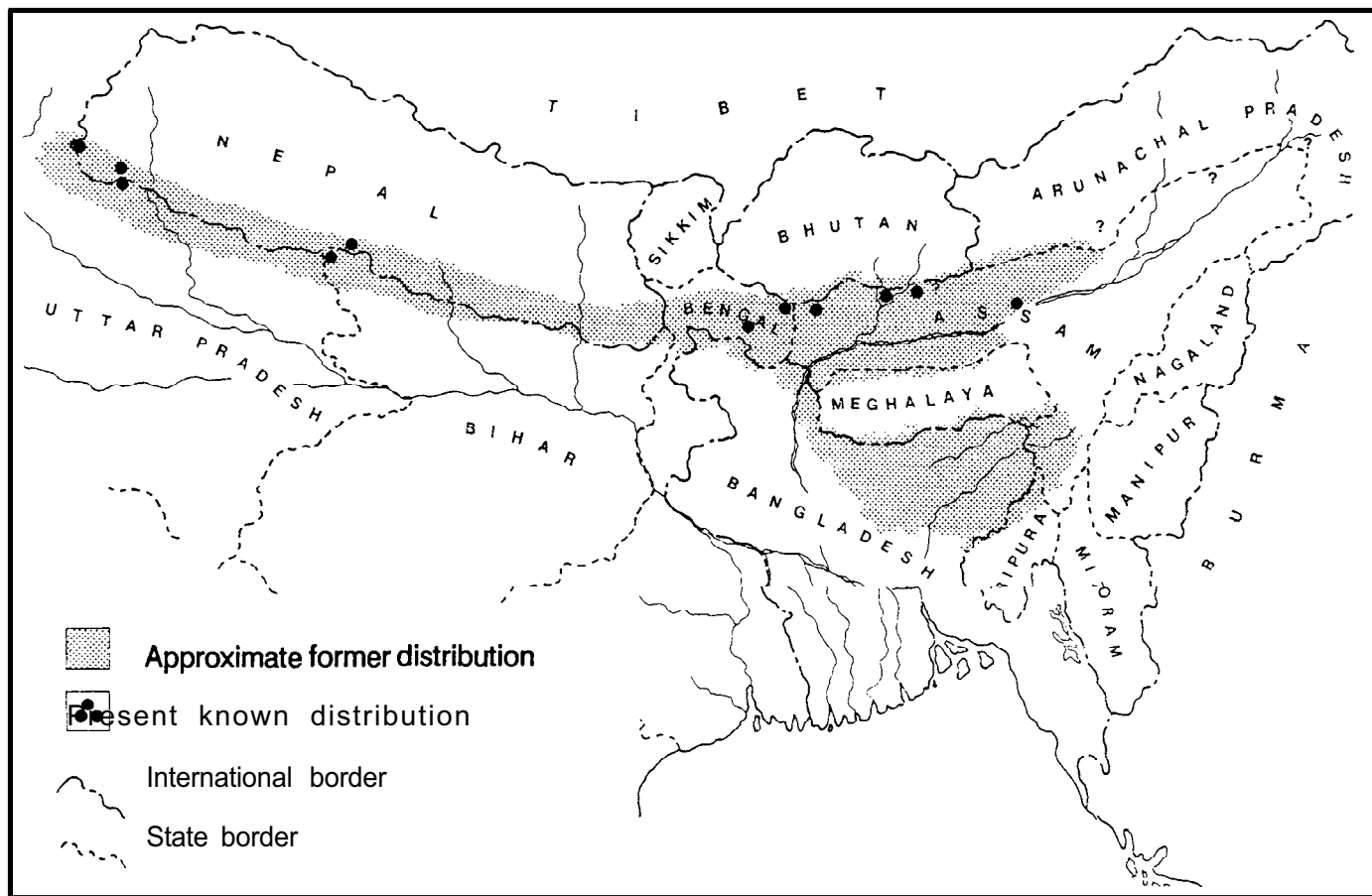


Figure 9.1 The sites indicated as still supporting hispid hare populations are (from west to east): Royal Suklaphanta Wildlife Reserve and Royal Bardia Wildlife Reserve (southwestern Nepal); Dudwa National Park (northeastern Uttar Pradesh); Valmiki Wildlife Sanctuary (northwestern Bihar); Royal Chitawan National Park (southern Nepal); Jaldapara Wildlife Sanctuary and Buxa Tiger Reserve (northern West Bengal); Ripu Reserve Forest, **Manas** Wildlife Sanctuary, Subankhata Reserve Forest and Orang Wildlife Sanctuary (northwestern Assam). The question marks indicate the approximate location of sites where this species was known to occur until recently but where there is some doubt if it still survives (e.g. Barnadi Wildlife Sanctuary*, northwestern Assam), or areas where reports of its occurrence have not been confirmed (e.g. **Pakkui** Wildlife Sanctuary, southwestern **Arunachal Pradesh**). Recent evidence for the presence of this species in Kanha National **Park** and other areas outside the known or postulated recent range of this species have not been included, since these reports have not yet been investigated properly. *The hispid hare was confirmed as present in the Barnadi Wildlife Sanctuary during February 1990.

wan National Park, Royal Bardia Wildlife Reserve and Royal Suklaphanta Wildlife Reserve in the Terai area of southern and southwestern Nepal (Oliver 1984). An earlier survey by Rands, et al. (unpubl. 1979) found no evidence of the continued survival of the hispid hare in the Terai region of southeast Nepal.

Other areas outside the known recent range, for which there is some evidence that the species may occur are listed in Table 9.2. The report of *Caprolagus* in Kanha National Park is based on the analysis of faecal pellets (see Oliver 1984 for techniques) and has yet to be confirmed by sightings. Since Kanha National Park lies approximately 500km south of the limits of its previously understood range, this report has important implications with respect to both the postulated former range, and its possible survival in intervening areas.

Habitat

Almost all recent data indicate that the hispid hare is dependent on the early successional **riverain** communities, typically comprising dense tall grasslands, commonly referred to as elephant grass or thatchland. These grasslands are a feature of the succession between primary colonizing grasses, (particularly tall grasses, on new alluvium deposited by changing water courses), through deciduous **riverain** forest to the sal (*Shorea robusta*) forest climax. Tall grassland may also form an **understorey** during later stages of the succession, particularly near rivers, or in forest clearings and abandoned cultivation and village sites. In relatively undisturbed areas, the tall grasslands are maintained by prolonged inundation during the monsoon or by periodic burning; in disturbed areas, they are **main-**

tained by regular burning, grazing, or regular harvesting for thatch and domestic animal fodder.

There are many species of tall grasses, which dominate in different situations. Dhungel(1982) identified eleven principal tall grass species in the Royal Chitawan National Park. In the same area, Laurie (1978) distinguished four main types of grassland: *Themida villosa*, which forms stands of up to six metres in clearings in sal forests, especially near old water courses; *Saccharum-Narenga* associations, which grow as pure or mixed stands up to eight metres high (of which the most important communities are those dominated by *S. spontaneum*, a primary colonizer of new alluvium; and *S. munja*, *Erianthus ravennae* and *Narenga* spp., which form characteristic stands during successional stages on well-drained ground, often with shorter grasses between them); *Arunda-Phragmites* associations, which form dense stands up to seven or more metres high on marshy ground and around lakes; and *Imperata cylindrica*, which grows as shorter stands, especially on sites formerly occupied by villages.

The hispid hare evidently utilizes all of these and other communities: e.g. those dominated by *Alpinia alughas*, *Typha elephantum*, *Cymbopogon* spp. and *Lea crispa* (an exotic and highly invasive herbaceous perennial) in Jaldapara Wildlife Sanctuary (Oliver 1984). These communities are of varying importance to the species at different times of the year, according to the availability of cover. During the dry season, most of these communities in most areas are subject to extensive, regular (controlled or uncontrolled) burning. Burning deprives the animals of cover and all other resources until the regrowth of vegetation, which follows the onset of the early rains a few weeks (or even up to two or three months) later. During this period, the animals are obviously entirely dependent on any cover left unburnt, e.g. marshy sward, usually dominated by *Phragmites* and *Arundo* spp., and/or *S. spontaneum* along river banks which are maintained by later, prolonged inundation and are therefore usually left unburnt. It remains unclear whether these are preferred habitats, or are used in the absence of cover elsewhere during the post-burning period. Equally, from the clear evidence of older faecal deposits exposed by the burning, other communities are inhabited by hispids at other times of the year.

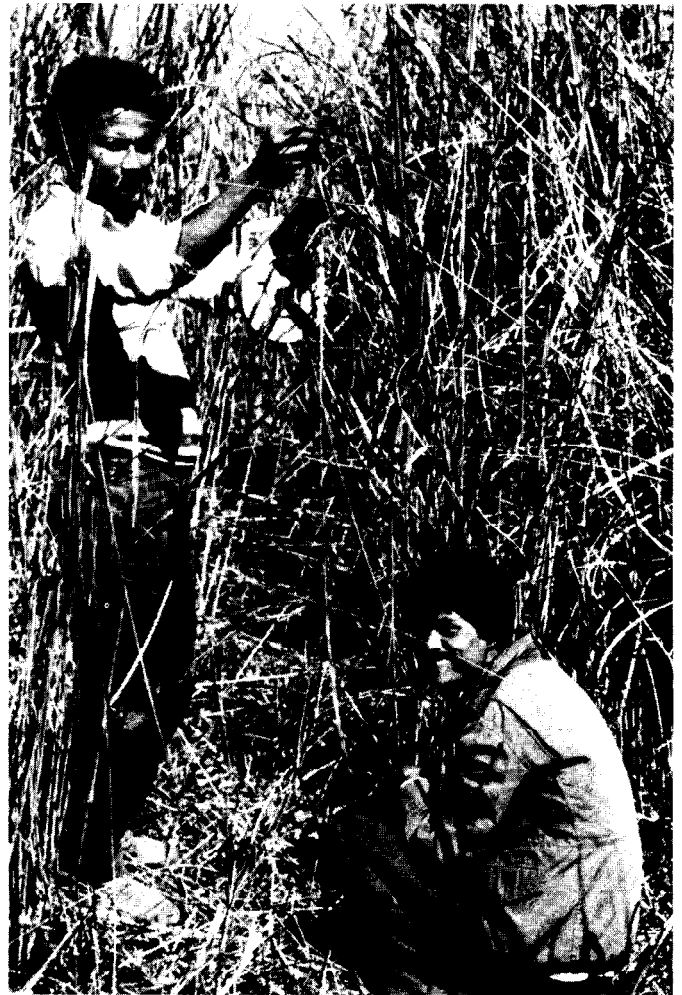
Behavior and Reproduction

The results of a recent three-month study of the behavioral ecology of the hispid hare (Bell 1986, 1987) suggest that the species is both structurally and behaviorally more of a rabbit than a hare. Unlike the more typical long-limbed and solitary hares, such as the Indian hare which ranged over larger areas of open short grassland, scrub and forest, the short-limbed hispids were restricted to small home ranges (mean areas of 8,200m² for males and 2,800m² for females) within the dense cover provided by unburned tall grassland.

Overlapping home ranges revealed by radio-tracking suggested that these animals were living as pairs, although the

total home range of individual males was larger than that of individual females. Two of the three females captured were pregnant, showing that the species is breeding during January and February in the western Nepal Terai. The uniformly small size of the scrotal testes in the males could suggest a monogamous mating system (Bell 1987).

The single fetus found in a pregnant female hispid during the above study, the single infant born to a female captured in Assam in 1976 (Oliver 1980) and the four nipples found in all females captured at Royal Suklaphanta Wildlife Reserve instead of the six reported by Blandford (1888), suggest that hispid hare litters may be small in size. Further research is required to determine whether *Caprolagus* has the altricial pattern of most 'rabbit' species or the precocial pattern found in *Lepus* (Cowan and Bell 1986). The hispid hare may show an intermediate strategy as reported in the swamp rabbit *Sylvilagus aquaticus*, forest rabbit *S. brasiliensis* and volcano rabbit *Romerolagus diazi*, which also live in similar habitats and rear young in surface nests situated in dense cover after a relatively long gestation (37-43 days); the young being well-developed at birth and leaving the nest fairly early.



Hispid hare habitat
(Photo by Diana Bell)

Table 9.1 Sites within known recent range of distribution of the hispid hare *Caprolagus hispidus*

Country/State investigated or reported	District/Location	Last date (s)	Source	Comment
Nepal	Royal Sukla Phanta Wildlife Reserve	1984/5/6	Oliver 1984, Bell 1986	See text
	Royal Bardia Wildlife Reserve	1984	Oliver 1984	“ “
	Royal Chitawan National Park	1984/5	Oliver 1984, Bell 1986	“ “
	Koshi Tappu Wildlife Reserve	1978/9	Rands <i>et al.</i> 1979	No evidence of continuing existence found by U.E.A.expedition. Remaining grasslands seriously degraded and/or flooded.
	Koshi Barrage	1978/9		
Uttar Pradesh	Pilibhit Forest Division	1984	Oliver 1984	Formerly extensive tall grasslands in Khatima and Puranpur districts, which almost certainly supported this species until recently, now seriously reduced by encroachment and irrigation/flood controls. No evidence of continuing existence of <i>Caprolagus</i> found during 1984 field survey.
	Kishanpur Wildlife Sanctuary	1984	Oliver 1984	Remaining grasslands subject to uncontrolled burning and grazing pressure from domestic stock. No evidence of <i>Caprolagus</i> found during 1984 survey, though it would be surprising if the species did not (formerly?) occur here.
	Dudwa National Park	1984	Oliver 1984	See text
	Katerniaghat Wildlife Sanctuary	1984	Oliver 1984	As Kishanpur
	North Gonda Forest Division	1984	Oliver 1984	Former tall grasslands along international border with southern Nepal now almost entirely replaced by later successive communities following the construction of irrigation/flood control barrages and canals during 1970's. No evidence of continuing existence of <i>Caprolagus</i> found during 1984 field survey.
Bihar	Valmiki Wildlife Sanctuary	1984, 1987	Oliver 1984	<i>No</i> evidence of <i>Caprolagus</i> obtained during 1984 survey, but subsequently reported by Ghose from the Tribeni Forest Block, in the core area of the Sanctuary (Ghose, in press).
West Bengal	Jaldapara Wildlife Sanctuary	1983, 1984	Ghose 1984, Oliver 1984	See text
	Buxa Tiger Reserve	1984	Oliver 1984	See text
Assam	Kochugaon Division	c. 1984	Oliver 1977	Most remaining grasslands in Kochugaon and Ripu Reserve Forests subject to regular uncontrolled burning. <i>Caprolagus</i> not believed to survive in this area, until a specimen was captured in mid-1980's (P. Lahan pers. comm. 1987).

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Table 9.1 contd . . .

Country/State investigated or reported	District/Location	Last date (s)	Source	Comment
	Haltugaon Forest Division	1977	Oliver 1977	<i>Caprolagus</i> reported to occur in tall grass lands along the northern boundary of Manas Reserve Forest, in areas contiguous with the Manas Wildlife Sanctuary.
	Manas Wildlife Sanctuary	1987	Various	Perhaps the single most important surviving population, <i>Caprolagus</i> was first reported in Manas 1977 shortly after the species' re-discovery in Mangaldai District in the same year. Found in suitable habitat throughout the Sanctuary, and reported to be increasing in numbers in some areas (S. Deb Roy pers. comm. 1987).
	North Kamrup Division	1977, '81, '87		<i>Caprolagus</i> reliably reported or definitely known to occur until recently in each of the four Reserve Forests comprising this Division, i.e. (from west to east): Subankhala, Darranga, Barnadi and Khalingdanaur Reserve Forests. Of these, Barnadi has assumed prominence as being the source of the original 'reappearance' of this species in 1971, and was declared a Wildlife Sanctuary in 1982. However, there is some doubt whether the species still survived in this area at that time, and it has not been reliably reported since 1977. The species was almost certainly extinct in Khalingdaur R.F. by 1975 or 1976. There is no information on its current status in Darranga R.F., but the species is known to survive in Subhankata.
	Orang Wildlife Sanctuary	1981	Oliver 1984	First reports of this species obtained in 1981 (P.C. Das, pers. comm.), subsequently confirmed by the capture of a single individual on the western boundary of the Sanctuary later that year.
	Darrang Division	1977	Oliver 1980	It is likely that <i>Caprolagus</i> occurred until recently at intervals along the northern boundary of this Division, which comprises a semi-continuous series of seven Reserve Forests and Wildlife Sanctuary, i.e. Sonai Rupa Sanctuary. However, the species was definitely known only from Gohpur Reserve Forest, at the eastern end of the forest belt, where it is now extinct following the destruction of the Reserve by illegal settlers between 1979 and 1981.
	Goalpara Division	1956	IUCN 1974	Evidence of this species' former occurrence between the Brahmaputra River and the Meghalaya State border is based on the collection of a single specimen in Goalpara District, by a German expedition in 1956. Although no systematic investigation has been conducted since that time, the species is assumed to be extinct south of the Brahmaputra River, following the destruction of the former tall grasslands in this region (S. Deb Roy, pers. comm. ; P. Lahan, pers. comm.).

contd...

Table 9.1 contd...

Country/State investigated or reported	District/Location	Last date (s)	Source	Comment
Bangladesh	Jamalpur and North Mymensingh District	1980	Khan 1982, Oliver 1984	Historically reported from a number of imprecisely recorded sites, but generally considered extinct in Bangladesh since the 1920's; a single specimen was reported to have been captured in the Mymensingh District in 1980. This specimen was taken by Dhaka University, but its identity remains in doubt and present whereabouts of this specimen is not known. No certain evidence of the continued existence of this species on northern Bangladesh was obtained during the course of the 1984 field survey of these and neighbouring areas.
	Dhaka District	1974	Khan 1982, Oliver 1984	Only recent report based on a single specimen collected in this District in 1974, but the precise origin of this specimen and its present whereabouts are unknown, and its identity has never been confirmed. No evidence of this species in Dhaka or neighbouring parts of south Sylhet District were obtained during the 1984 field survey.

Population and Threats to Survival

No attempt has been made to estimate population numbers, but there is no doubt that the species has declined dramatically in recent years as a result of the loss of its tall grassland habitat (see below) to agriculture, commercial forestry, flood control schemes and human settlement. The few pockets of tall grassland habitat which remain all lie within National Parks, Wildlife Reserves and Sanctuaries scattered across the former distribution tract and the surviving populations listed above have been found as a result of searches within these dispersed areas (Oliver 1980, 1984; Ghose (in press). While the survival of these populations is encouraging, it is important to emphasize firstly that these areas represent only a small percentage of the total number visited (see Tables 9.1 and 9.2), and secondly that these isolated, relict hispid populations remain at risk because of the continuing degradation of habitat even within these protected areas by overgrazing by domestic stock, human exploitation of thatch and cane material, and the often uncontrolled, regular burning of grassland during the dry season (Oliver 1984, Bell and Oliver in press). The long-term survival of the Buxa population, for example, was deemed unlikely given the heavy overgrazing of available habitat by domestic stock (Oliver 1984).

The behavioural ecology of hispid hares at Royal Suklaphanta Wildlife Reserve, western Nepal, (Bell 1986, 1987) suggests that the population carrying capacity of these areas may be determined by the extent of those small patches of tall grassland which escape the annual (sometimes biannual) early dry season burning. During searches from January

to March, fresh hispid hare sign was found only in small pockets of tall riverine grassland which had escaped the early dry season burning by virtue of its marshy location. The home-ranges of radio-collared animals were entirely restricted to these narrow strips of tall, marshy riverine sward during these months. The estimated density in unburned tall grassland (1/1,470m²) again reflects their confined distribution within the few islands of refuge cover available at a time when the species was also breeding. The fate of two of the radio-tracked hispids suggests that their enforced concentration within these isolated patches of post-burn cover may also increase their susceptibility to predation. Both animals had been cached by Indian foxes *Vulpes bengalensis* or golden jackals *Canis aureus*, one having first been killed by another, possibly avian predator.

This three-month study of distribution during the post-burn period clearly needs to be followed up by further investigations into the distribution of the animals during the rest of the year, particularly during the monsoon period when the marshy post-burn refuge areas are likely to be amongst the first to become inundated.

Many of these areas are subject to illegal grazing of domestic cattle and buffalo by local villagers. It is estimated that over 1,000 such animals enter daily to graze in Royal Suklaphanta Wildlife Reserve (S. Bajimaya, pers. comm.). The damage caused by livestock is not restricted to grazing and trampling, since they are also known to introduce diseases to resident wild species (Poppleton and Shah 1977), and more significantly perhaps, much uncontrolled burning to promote fresh grazing pasture is carried out by the graziers. The

Table 9.2 Sites outside known recent range of the hispid hare *Caprolagus hispidus*, from which (unconfirmed) reports have been obtained

Country/State investigated or reported	District/Location	Last date (s)	Source	Comment
Bihar	Rajamhal	1981	Ghose (unpubl.); Oliver 1984	A number of independent reports from Rajmahal Hills, received in 1981 but not yet investigated
Madhya Pradesh	Kanha National Park	1984/5	Oliver 1984; Bell <i>et al</i> , in prep.	See text
Meghalaya	Garo Hills	1984/5	S.K. Chenda pers. comm.; Oliver 1984	Several, apparently reliable reports obtained by Zoological Survey of India between 1982 and 1984, but not confirmed during subsequent visits by Ghose, who also notes the absence of any apparently suitable habitat over most of this region. A further survey is proposed during 1988/89.
Arunachal Pradesh	Pakkui Wildlife Sanctuary	1983	L.K. Mehta in <i>litt.</i> ; Oliver, 1984; Ghose (unpubl.)	Various unconfirmed reports from Pakkui area, including an account of two hispid being captured by a D.F.O. stationed at Seijusa in November 1983. However, the identity of these animals has not been confirmed, and these reports await further investigation.
Arunachal Pradesh	Kobo-Pasighat and Tirap Districts	1979/81/84	A.K. Mukherjee pers. comm.; Oliver 1984; in <i>litt.</i>	Various reports from areas of surviving grass lands on either side of the Upper Assam and northeastern A.P. border. In particular, grasslands in the conjunction of the Dihang, Dibang and Lohit Rivers, where A.K. Mukherjee obtained convincing report of <i>Caprolagus</i> in 1979. These include grasslands in the contiguous Lali Wildlife Sanctuary (Tira District, A.P.) and Dibru Saikhowa Wildlife Sanctuary (Dibrugarh District, Assam), which would merit further investigation; as might suitable areas in the Dibru Reserve Forest and Namdapha Tiger Reserve.

adverse effects on tall grasslands of illegal grazing in combination with regular burning are discussed by Bell and Oliver (in press).

Apart from Dudwa National Park, where the tall grasslands are pre-emptively burned by Park staff to prevent casual burning later in the dry season, the annual burning in the other areas listed above is primarily undertaken by thatch-collectors. Burning of the typical thatchland grass species, such as *Saccharum*, *Imperata*, *Themeda* spp. facilitates the exploitation of thatch and cane materials by removing leaves and dead material so that the flowering culms can be harvested more easily. In Dudwa, Chitawan, Bardia and Suklaphanta, thatch is collected by villagers during selected periods, under varying degrees of supervision and after payment of nominal admission fees. However, adequate supervision of the large numbers of people involved (e.g. approx. 10,000 at Dudwa and

80,000 to 90,000 at Chitawan) is problematical and expensive to organize and police.

Extensive flood control proposals threaten the ecological diversity of several of the above areas of tall grassland. For example, the hispid hare population in Royal Bardia Wildlife Reserve would be seriously affected by the proposed dam to be built across the Karnali River (Oliver 1984) .

Conservation Measures Taken

The species is accorded maximum protection under Schedule 1 of the Indian Wildlife Protection Act 1972 and is also listed under Appendix I of CITES. The several attempts to delineate the distribution of *Caprolagus* and determine its management

needs were referred to above (Oliver 1979a, 1979b, 1981, 1984, Ghose in press, Bell 1986, 1987, Bell and Oliver in press).

Conservation Measures Proposed

Recommendations submitted to the Government of India, concerning the need for status surveys of the tall grasslands in north-eastern India not previously investigated, have been agreed but not yet implemented.

A shift from uncontrolled dry season burning to careful rotational burning, such that large areas of suitable cover and food are available throughout the year, may alleviate the immediate risks for relict populations of the species. In Dudwa National Park, there are plans to reduce controlled burning from an estimated average of 75% available grassland burned per annum to around 60% on a rotational basis, while in Jaldapara, the stated objective of rotationally burning approx. 33% of grasslands per annum has been frustrated by continued casual burning in excess of that amount (Oliver 1985).

However, long-term research programs examining the effects of each of the several disturbance factors (e.g. burning, thatch harvesting, and grazing) operating on this habitat are required to formulate appropriate long-term management plans for these remnants of tall grassland. Research into burning, for example, should investigate the effects of factors such as timing, frequency and soil water content on both the vegetation and resident populations (Bell and Oliver in press), so that optimum management plans can be developed for individual areas.

Further long-term studies of the behavioral ecology and reproductive biology of the species are urgently required. Effective protection and long-term management of tall grass-shrub habitat would also benefit sympatric endangered species, such as the pigmy hog *Sus salvanius*.

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Chapter 10: The Sumatran Rabbit *Nesolagus netscheri*

John E.C. Flux

Status and Summary

The Sumatran rabbit *Nesolagus netscheri* (Schlegel 1880) is apparently the rarest lagomorph. About a dozen museum specimens exist, collected between 1880 and 1916, and there has been only one confirmed sighting since then, in 1972. It has always been a rare animal, living at 600-1,600m in dense forest, much of which has been cleared for tea and coffee plantations. Forest clearing is continuing rapidly as people settle in Sumatra from Java. An extensive mammal survey in 1984 found only three areas where locals knew of rabbits and none were seen. Visits to two of these areas in 1989 indicated that in one there was confusion with feral European rabbit *Oryctolagus cuniculus* and the other had been cleared of forest. Discovery of a population and its protection pending a widespread survey for the rabbit is extremely urgent.

Description and Taxonomy

The Sumatran rabbit is about the size of a European rabbit (1.5kg), head and body length 368-417mm, tail 17mm, hind foot 67-87mm, ear 34-45mm, skull length 67-74mm. Apart from the very short ears, this rabbit is immediately distinguished by its wide black or dark brown stripes on a yellowish grey background that becomes rusty brown towards the rear. The fur on the underparts, below the chin and on the inside of the legs is whitish. The ears are black, and when folded forward reach only to the eye. Compared with a European rabbit, the head is broader and the muzzle shorter, and the legs are also shorter. The tail is so short that it is normally not visible and contains only 12 bones compared to 19-24 in other leporids. The fur is soft and rather short, and the delicate skin is easily damaged. According to Jacobson and Kloss (1919) the coloration is very variable between individuals, with the stripes being absent in the front or much reduced.

Taxonomically the Sumatran rabbit was first described under *Lepus* and given a separate genus by Forsyth-Major (1899). The relationship with other leporids is very distinct and it is regarded as a primitive form with no close relatives, which is supported by the fact that it carries a unique genus of flea, *Nesolagobius* (Hopkins 1957).

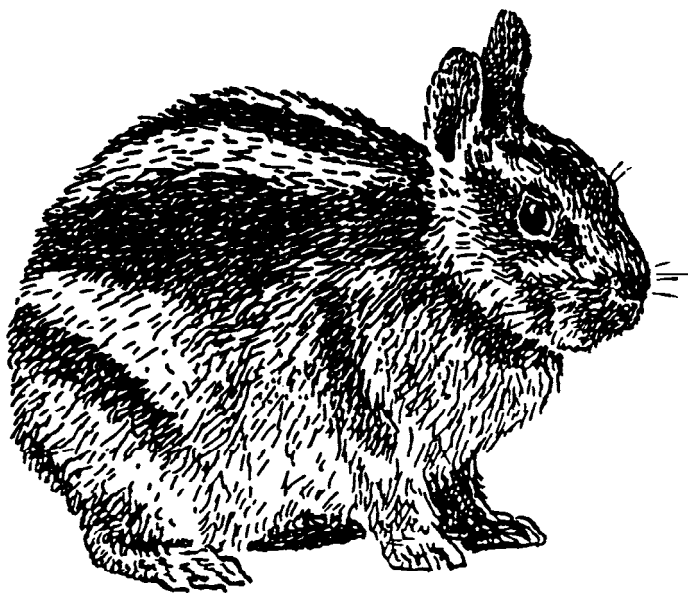
Distribution

The Sumatran rabbit is restricted to montane forest in the Barisan Mountains, west and southwest Sumatra, with one recent record by Dr. M. Borner in 1972 from Gunung Leuser

National Park, northwest Sumatra, and a possible sighting by Dr. J. Seidensticker near Mt. Kerinci in 1978. Nearly all the records are from coffee or tea estates where rabbits were seen as the forest was felled, between 600m and 1,600m. It is completely nocturnal and lives only in remote forest, which may explain why local people have no name for it and are unaware of its existence, and it could be more widespread than the seven known locations indicate (see Fig. 10.1). On the other hand, forest clearance by man has been going on for at least 7,500 years, perhaps 17,800 years (Maloney 1980), there are now over 20 million people on the island, and detailed surveys for other rare species (tiger, Sumatran rhino) have not encountered any rabbits, so they seem to be remarkably rare animals.

Habitat and Ecology

In the original description, it was stated that the Sumatran rabbit lived in woods and rice fields, but the latter is certainly wrong (Jacobson and Kloss 1919). The habitat is montane forest on rich volcanic soil, and it feeds on plants which form forest understorey, not in openings or clearings. The preferred diet was *Cyrtandra*; Jacobson does not say which species, but 35 occur on Sumatra and ten on Mt. Kerinci where rabbits live (Ridley 1917). *Aracea* (*Homalomena*) was accepted; and *Synedrella nodiflora*, *Ipomoea batatas*, *Jussiaea suffruticosa*, *Polygonum*, *Tradescantia*, *Elatostemma*, *Hemi-*



Sumatran rabbit, from photo by E. Jacobson

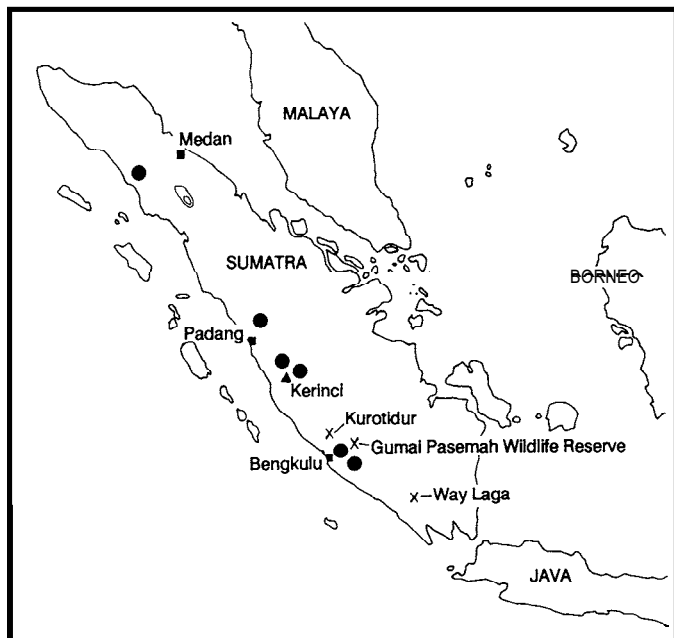


Figure 10.1 Map of all known specimens of the Sumatran rabbit (circles) and the three locations where they were reported in 1984 (crosses).

graphis colorata and *Trifolium* spp. were eaten reluctantly. Cultivated vegetables were not accepted, nor were roots or the bark of trees. Captive rabbits took readily to cooked rice, young maize, bread, ripe bananas, and sometimes pineapple (Jacobson and Kloss 1919), and one kept in the Amsterdam Zoo, August-September 1895, ate beans, radishes, carrots, bread, and young shoots of oak, elm, and beech (Jacobson 1921).

Behavior

The Sumatran rabbit is nocturnal and hides during the day in dark places at the base of trees, in burrows, or holes in the ground. Because in captivity it did not dig in the ground, Jacobson and Kloss (1919) thought it probably used burrows made by other animals. All their specimens were snared at night in holes in brush “fences” made by trappers. Captive rabbits were slow moving compared with European hares, and fed only at night, spending the day nearly motionless.

Reproduction

Nothing recorded.

Remarks

Considering that the Sumatran rabbit is only active at night, and lives in remote, inaccessible habitat, it may not be surpris-

ing that local people had no name for it when it was discovered. However, it appears never to have been abundant anywhere in its range: Dr. M. Borner saw only one in 450 days of field work on rhino in Gunung Leuser National Park, and a well-organized expedition in 1914, employing seven collectors who spent several months trapping on Mt. Kerinci, did not catch any rabbits (Robinson and Kloss 1936). Whitten *et al.* (1984) say “This species has not been reported since 1937 but the CRES team found that some farmers on the lower slope of Mt. Kerinci still see it very occasionally.”

A thorough survey for many rare mammals was carried out in 1983 and 1984 by Blsueh (1984), who states: “We never encountered any direct evidence of Sumatran hares but we did find three places where local people described the animal well enough for us to conclude that it occurs there. In the settlement of Way Laga south of Liwa on the border of Bukit Barisan Selatan National Park it was reported that a group of four including small ones was once seen near the edge of the forest in recently cleared land that was about to be planted with coffee. People living on both the north and south sides of the Gumai Pasemah Wildlife Reserve in Sumatra Selatan say that hares are fairly common in the reserve at an altitude of around 1,600m, and one was once caught and killed by a dog . . . villagers claim that no one bothers to hunt the hares. People in the town of Kurotidur in Bengkulu about 40km north of the provincial capital also report that there are hares in the mountainous protection forest east of the village.”

“It seems that hares are sparsely distributed throughout the length of the Barisan Mountain chain in southern Sumatra. Their survival depends on the continued existence of their mountain forest habitat. Whether or not they can live in disturbed forests is a moot point since in mountainous areas there is little selective timber cutting: either the forest remains in a more or less undisturbed condition or it is cut down completely and converted to agriculture. They apparently are not subjected to much hunting pressure, probably because they naturally occur at such low densities and in such remote areas that it is not worth the effort to hunt them.”

In July 1989 two of these areas were revisited. We found that people living north of the Gumai Pasemah Wildlife Reserve had confused the Sumatran rabbit with a feral colony of European rabbit living in a coffee plantation, while the Kurotidur area is now largely cleared of forest.

A 5-year project, “Conservation of Sumatran hare *Nesolagus netscheri*”, was designed in 1979 and submitted to IUCN/WWF by Dr. K. Myers, but funds were not available at that time. In the meantime forest has continued to be cleared, often with World Bank funding, for land to grow cocoa (Dr. C. Santiapillai, pers. comm. 1989). The discovery of a viable population of Sumatran rabbits, and its protection, is the first necessary step. This should be followed by a thorough survey to determine the status of the rabbit in other existing reserves, and in the remaining unreserved forest habitat.

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Chapter 11: The Amami Rabbit *Pentalagus furnessi*

Ken Sugimura

Status and Summary

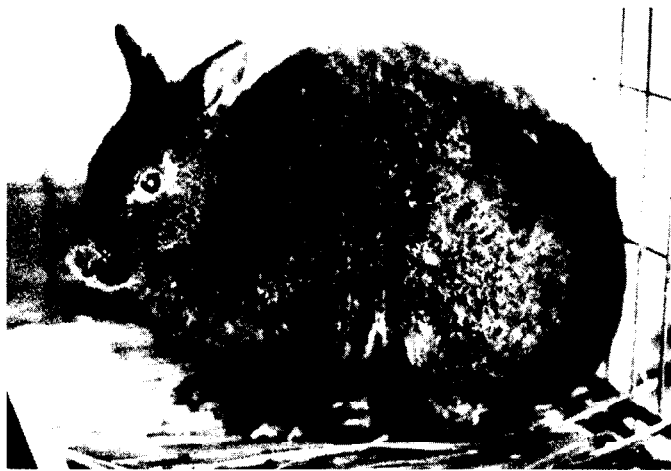
This species is endangered. The Amami rabbit *Pentalagus furnessi* (Stone 1900) is designated as a special natural monument by the government, but even its existence is not widely known among the people of Japan. The population is protected from hunting, but little attention has been paid to the management of its habitat. Scientists recognize the rabbit as one of the living fossils, because its morphological traits are similar to fossil species found in the Miocene stratum.

Description and Taxonomy

Recognized as one of the most primitive lagomorphs in the world, it is most obviously distinguished from other species of lagomorphs by its dark fur. The Japanese name, **Amaminokurousagi**, denotes “the black rabbit of Amami”. It differs from typical lagomorphs (*Lepus*, for example) by having small eyes and ears, a long snout and short limbs with relatively large nails for digging nest holes. External measurements are: body length, 418-470mm; tail length, 11-35mm; ear length, 41-45mm; and hind foot, 85-92mm (without nails).

Distribution

The species is found only on Amami Oshima and Tokuno-shima, two islands forming part of the Ryukyu Archipelago (areas 819.89 and 248.43km², respectively) (Fig. 11.1).



Amami rabbit *Pentalagus furnessi* (Photo by Ken Sugimura)

Population Size

A population estimate based on field observations was made only once on Amami Oshima, giving a total population of 6,000 on the island (Anon. 1977). However, this estimate was based on a small number of observations and the study area was located in the part of the island where density of rabbits was high compared to other areas (Sugimura 1987). The 1977 investigation made pellet counts on three kilometres of forest roads over two days and found 72.25 pellets/km/day on average. Sugimura (1987) counted 38.5 pellets/km/day for the same season on 50.25km of forest roads during 78 days of observations. Revising the previous estimate, Sugimura (1987) calculated the number of rabbits on Amami Oshima to be 3,750. The figure may be still an overestimate, because the area covered by the study had a higher frequency of rabbit tracks on average than other forest sites.

The population size on Tokuno-shima has never been estimated. The area of suitable forest habitat on Tokuno-shima is 111.2km², while the forest area on Amami Oshima is 693.78km² (Anon. 1988). If the same density of rabbits is found in the forests on the two islands, the population size on Tokuno-shima would be roughly one seventh of that on Amami Island; less than 500. However, Sugimura (1987) indicated that rabbits were absent from areas close to human settlements. Because of the smaller forested area on Tokuno-shima, a larger proportion of the forest is located close to settlements compared to Amami Oshima. Therefore, the habitat quality is poorer and average density is expected to be lower on Tokuno-shima.

Habitat

Rabbit signs are found in forests of all successional stages but not in cultivated or residential areas (Anon. 1977, Anon. 1984, Sugimura 1987). Early investigators postulated that these rabbits live in primary forests, probably because the islands were originally covered by dense natural forests (Imaizumi 1968, Yasuma 1984). The rabbit's dark coloration may be related to the darkness of the forests they inhabit (Imaizumi and Okada 1960). Recent observations indicate that rabbits are also found in cut-over areas and forest edges covered by the Japanese pampas grass *Miscanthus sinensis* (Suzuki 1985, Sugimura 1987). Sugimura (1987) found droppings most frequently along forest roads that ran through young secondary forests and that the boundaries between young forests and primary forests were frequently used in winter.



Original forest habitat and recently cleared forest on Amami Oshima (Photo by Ken Sugimura)

Food

Field signs have indicated that these rabbits feed on leaves of the Japanese pampas grass *Miscanthus sinensis*, runners of the Japanese sweet potato *Ipomoea batatas*, bamboo sprouts, acorns of the pasania tree *Castanopsis sieboldii* and the bark of forest trees; *Ficus erecta* (Moraceae), *Podocarpus macrophyllus* (Podocarpaceae), *Psychotria serpens*, *Mussaenda parviflora*, *Gardenia jasminoides* (Rubiaceae), *Clerodendron tichotomum* (Verbenaceae), *Mallotus japonicus* (Euphorbiaceae).

Of these food items, *Miscanthus sinensis* is the most important in summer and acorns of *Castanopsis sieboldii* are probably the most important in winter in terms of nutrition. No quantitative studies have been conducted on the food habits of these rabbits. The relative importance of the various food items is unknown (Kirino *et al.* 1989).

Behavior

In general Amami rabbits are nocturnal. They frequently use passages through the undergrowth or climb up and down on steep slopes along forest roads. They make clicking sounds when communicating with each other. Burrows are used for dens and nests. Mating behavior most often occurs in November and December, and kits first appear above ground in April or May (Mr. Minami, pers. comm.).

Management

Rich undergrowth cover will provide abundant food for the rabbits, while short arboreal cover of young secondary forests provides suitable hiding places. Old forests yield acorns in fall. A mosaic of these different vegetation types will probably form the most suitable habitats for the rabbits. Extensive logging operations on the two islands have resulted in the area of old forests (selectively cut) being decreased to less than 5% of all the forests in 1980 (Sugimura 1987). Although young secondary forests may provide suitable habitats for the rabbits, preservation of old forests will be the most important means of preserving the species. Field signs indicate that feral dogs are the most important predators of the rabbits

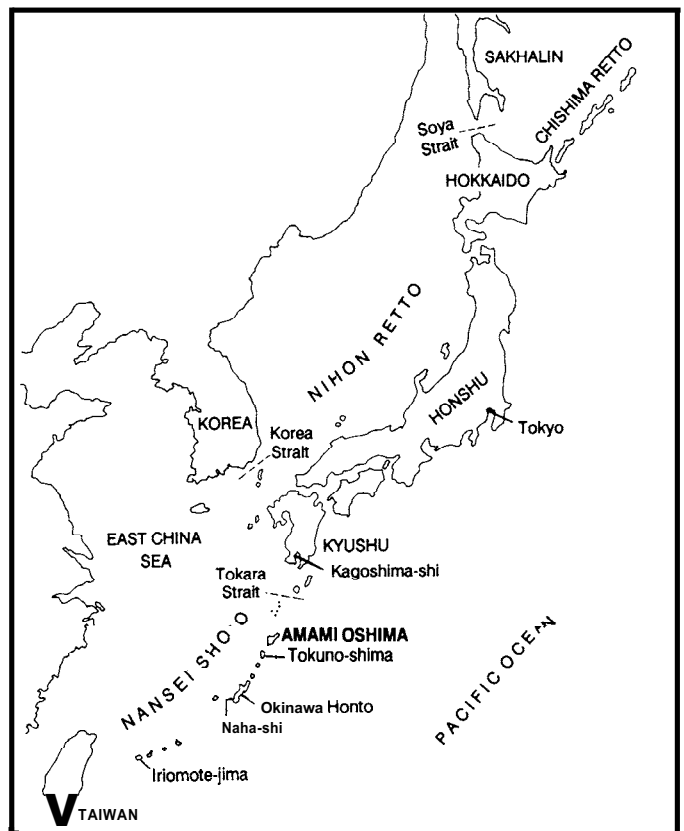


Figure 11.1 Amami Island and its vicinity

(Sugimura 1987). Mr. Minami (pers. comm.) stated that feral cats are the most important predators because they climb up and down cliffs without difficulty and do not allow the rabbits to escape. The distribution of pellets indicated that rabbits are almost absent from near human residences, where feral dogs and cats are abundant. Therefore, in addition to the preservation of old forests, removal of feral dogs and cats is critical to the preservation of the Amami rabbit. The conservation of the full range of habitats on Amami Oshima is also important for the other endemic species that occur there: 17 species of reptiles and amphibians two rats, two birds, 20 plants and a large number of invertebrates.

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Chapter 12: The Volcano Rabbit *Romerolagus diazi*

John E. Fa and Diana J. Bell

Status and Summary

The volcano rabbit *Romerolagus diazi* (Ferrari-Perez, 1893) is Endangered. Its distribution now restricted to three discontinuous areas of core habitat covering a total of approximately **280km²** on the slopes of four volcanoes (Popocatepetl, Iztaccihuatl, El Pelado and Tlaloc) in central Mexico. Threatened by habitat destruction through forest fires, encroaching agriculture and property developments. Although the hunting of the volcano rabbit is now illegal, this legislation is not enforced and the species is still hunted together with two sympatric *Sylvilagus* species.

Description

The volcano rabbit is considered by several authorities to be the most primitive of the living rabbits and hares (De Poorter & Van der Loo 1981, Corbet 1983). It is a small rabbit (adult weight around 500g.), being larger than only the pygmy rabbit *Brachylagus idahoensis* amongst the Leporidae (Nelson 1909). Hind legs and feet are short, ears small and rounded, tail inconspicuous. Pelage is short and dense, dorsal and lateral parts dark brown to black. Sexual dimorphism is minimal, females being slightly larger than males.

Distribution

The volcano rabbit is endemic to central Mexico. A recent distribution survey (Bell et al. 1985, Hoth et al. 1987) in pine-zacaton habitat on volcanoes across the Transverse Neovolcanic Belt (TNB) found evidence of the species on the slopes of only four volcanoes - namely Popocatepetl and Iztaccihuatl (Sierra Nevada), El Pelado and Tlaloc (Sierra Chichinautzin). Volcan Tlaloc is situated 40km west of Popocatepetl and El Pelado just 20km west of Tlaloc (Figure 12.1). The present distribution of the volcano rabbit is currently restricted to three discontinuous areas of core habitat which together cover a total of around 280km² (approx. 146km² around Popo/Izta, and 48 and 86km² around volcanoes Pelado and Tlaloc respectively). The results of that survey also suggest that the species has disappeared from areas of the central TNB zone where it had been reported in the recent past, for example, the eastern slopes of Iztaccihuatl (Rojas-Mendoza 1951) and the Nevada de Toluca (Granados 1981).

Population

No reliable estimates. Density of animals is possibly high in certain patches of “zacaton” within the core habitats, as reflected by the high density of latrines. A recent study (Fa et al. in prep.) shows a positive correlation between “zacaton” cover density and latrine density.

Habitat and Ecology

Volcano rabbits are found between 2,800 and 4,250m in elevation inhabiting pine forests (*Pinus*) with dense undergrowth of bunch grass (“zacaton”) and rocky substrates. Most of the areas where the rabbit is found have winter drought and summer rains with a mean annual precipitation of around 1,500mm. Cervantes-Reza (1980) records a mean temperature of 9.6°C, with the hottest month being May and the coldest January. The main volcano rabbit habitat is an open forest of *Pinus montezumae* and *Pinus hartwegi* up to 25m high, intermixed with other pine species (*P. rudis*, *P. teocote*, *P. patula* and *P. pseudostrobus*). There is usually a dense ground cover of tall, coarse, clumped “zacaton” grass, mainly *Muhlenbergia macroura*, *Festuca rosei*, *F. amplissima* and *Stipa ichu*. Herbs associated with these species are *Penstemon*

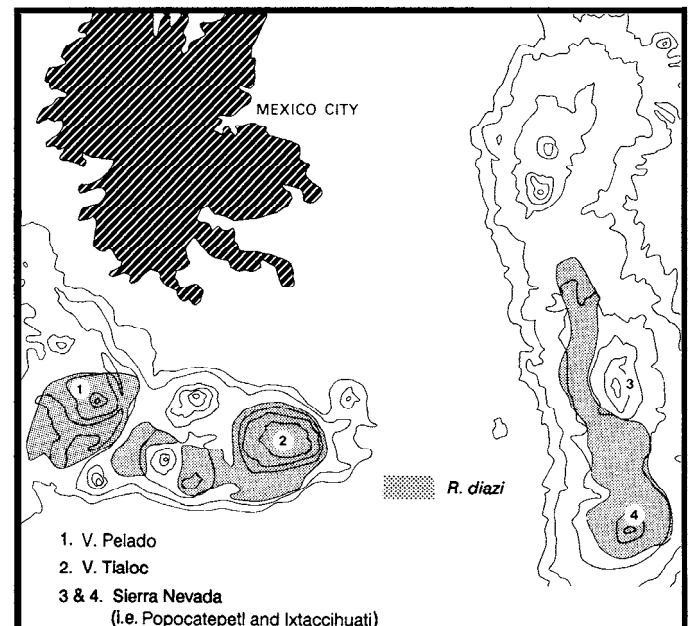


Figure 12.1 Present distribution of the volcano rabbit *Romerolagus diazi*



Volcano rabbit sheltering under Zacaton grass
(Photo by W. J. Bell)

stenophyllum, *Geranium potentillae*, *Stachys agraria*, *Lupinus montanus*, *Senecio salignus*, *Gnaphalium conoideum*, *Plantago patagonica*, *Bidens diversifolia*, *Alchemilla sebaldiaefolia* and *Museniopsis arguta*. The rabbit occurs in a variety of plant communities, from pure stands of pine with an understorey of bunch grasses through formations of dense secondary vegetation composed of alder *Alnus firmifolia* and *Senecio* spp. However, Bell *et al.* (1985) suggest that the scattered distribution of volcano rabbits within the above core areas correlate with density of cover of "zacaton".

Although some authors, like Cervantes-Reza (1980), discuss the use of burrows by the species, there is little evidence that the species is an active burrower. This characteristic is facultative since volcano rabbits live mostly on the surface under the dense cover of "zacaton" within runways made by the movement of animals. Cervantes-Reza (1980) reports the volcano rabbit as using abandoned pocket gopher, ground squirrel, armadillo and badger burrows. Females build nests in the wild and in captivity and have been observed to excavate a round cavity in the soil or amidst a "zacaton" clump (Cervantes-Reza 1980).

Feeding habits are largely unknown, but Cervantes-Reza (1980), Gaumer (1913) and Rojas-Mendoza (1951) report volcano rabbits feeding on "zacaton" grasses, especially *F. amplissima*, *S. ichu* and *Epicampes* sp. *Alchemilla sebaldiaefolia* and *Museniopsis arguta* are also food items. Volcano rabbits select the green and tender young leaves of grasses, biting the base and lower edges of the clump. Cervantes-Reza (1980) observed volcano rabbits feeding on young leaves of spiny herbs such as *Erynigium* and *Cyrsium*.

Main predators are longtailed weasels *M. frenata* (Cervantes-Reza 1981) and bobcats *Lynx rufus* (Romero 1988). Analyses of hair remains in bobcat scats revealed that volcano rabbits can be as much as 80% of the monthly diet (Romero 1988). Coyotes also prey on adult volcano rabbits (Cervantes-Reza 1981). Cervantes-Reza (1981) reports the case of two volcano rabbits being found in the digestive tract of a rattle-

snake. Red-tailed hawks *Buteojamaicensis* may also prey on the volcano rabbit.

Threats to Survival

Habitat destruction and hunting continue to threaten the survival of the volcano rabbit in the three core areas. Hunting is now illegal, according to the new national hunting laws, but enforcement is difficult.

A variety of agents appear to be responsible for the continuing erosion of the forest/zacaton habitat. These include forest fires, overgrazing by cattle and sheep, encroachment by agriculture and property developments, over-exploitation of timber and cutting of "zacaton" grasses for thatch and brush manufacture.

According to posters produced by the Forestry Department in a campaign to reduce forest fires, 98% of such fires are started by people. Many of these originate from uncontrolled burning of zacaton to promote new growth of pasture for cattle and sheep. Such excessive burning causes deterioration and depauperisation of "zacaton" habitats. Encroachment by agriculture from the surrounding villages into areas such as Volcan El Pelado is an increasing cause for concern. Land tenancy is undefined in El Pelado and Tlaloc areas. Villagers from Topilejo, Parres and other smaller villages can acquire rights to grow crops on Volcan El Pelado without prior assessment of impact on the land. Extraction of soil to depths of two metres and areas of up to one hectare is largely uncontrolled. Permits are issued by local village authorities, often without liaison with the conservation authorities.

Building developments in the Izta-Popo National Park pose a threat to surrounding habitat.

Each of the remaining volcano rabbit populations lies within 45 minutes drive of Mexico City, now the world's largest city, with a rapidly growing population of 20 million people. A substantial area of original volcano rabbit habitat has already disappeared as a result of expansion of the city. The threat of urban extension lies not only from the increase of Mexico City, but from the rapid increment in rural settlement areas around the core habitats.

Social Organization and Reproduction

Although groups of two to five animals have been reported (Rojas-Mendoza 1951, Cervantes-Reza 1980), the species' social organization has yet to be studied in the wild. Hoth and Granados (1987) report the formation of social dominance hierarchies amongst groups of six individuals (two males, four females) housed in semi-natural enclosures, with only one male and one or two females breeding in each group. Gaumer (1913) reports volcano rabbit groups of two to five individuals. Captive females were clearly aggressive toward both sexes, whereas males were never observed to initiate aggression

toward a female (Cervantes-Reza 1980, De Poorter and Van der Loo 1981). Female-female aggression was much more frequent and violent than female-male aggression. Dominant individuals were always females.

Captive Breeding

Volcano rabbits have been kept in captivity by five organizations (Faculty of Science, U.N.A.M.; **Antwerp Zoo**; Central Institute for Experimental Animals, Japan; Jersey Wildlife Preservation Trust and Chapultepec Zoo, Mexico City). At present, there are only three of these institutions holding colonies. These are Jersey (Durrell and **Mallinson** 1970, Lindsay 1982), Chapultepec and the Central Institute for Experimental Animals, Japan (Matsuzaki et al. 1982). The Chapultepec colony, where the animals are grouped in outdoor enclosures planted with clumps of "zacaton" grasses, bred particularly well for the first couple of years (Hoth and Granados 1987) but infant mortality has been very high. The captive breeding projects at Jersey and at **Antwerp Zoo** have been less successful (IUCN 1972), the latter having been recently terminated. In an attempt to emulate the **Chapultepec** accomplishment, similarly planted enclosures have been set up at Jersey Wildlife Preservation Trust (Bell et al. in prep.)

Conservation Measures

Listed under Appendix I of CITES (1973). Its hunting is now illegal under Mexican law, but this legislation is not enforced. Although part of its present distribution lies within protected areas (Izta-Popo and Zoquiapan National Parks), agents of habitat destruction, listed above, continue to operate in these areas. There is a proposal from Secretaria de Desarrollo Urbano y Ecologia (SEDUE), currently under review, to

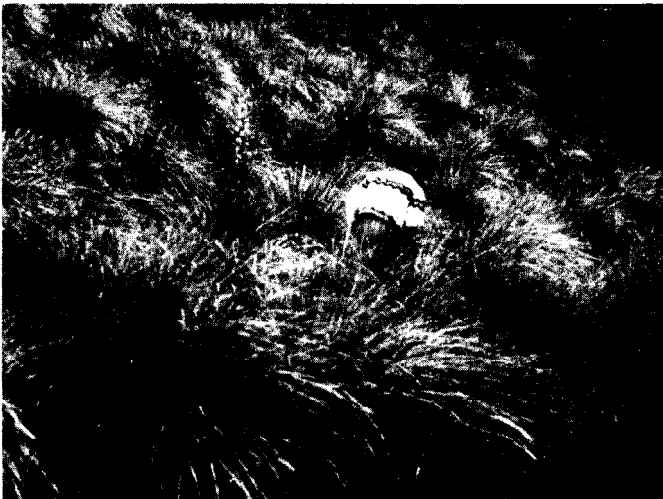
create a protection corridor from Tepozteco National Park, across the Chichinautzin range to the Desierto de los Leones National Park. This initiative would ensure the protection of buffer areas surrounding core zones for the species.

A fund to promote conservation work on the volcano rabbit and its habitat has been started by Dr. John E. Fa with the Centro de Ecologia at U.N.A.M., Mexico City. The fund was initiated **using** the proceeds from the sale of a poster depicting the species in its habitat.

Conservation Measures Proposed

The survival of the species clearly revolves around the management of burning and overgrazing in the prime "zacaton" habitats and the enforcement of laws that prohibit the catching, sale and hunting of the animal. The following are recommended conservation measures:

1. Forest areas where the volcano rabbit is found are significant not only for this species but also as a reservoir for other **endemics**. It is also an important zone for life-support systems in the Mexico City region. These forests are crucial as water catchment zones and can be exploited rationally for timber and other renewable resources. Emphasis on this point should be made in achieving protection of volcano rabbit habitats.
2. Within the protected areas and other zones with protection pending, appropriate management must start. The supervision given by the SEDUE or the **Comision Coordinadora de Desarrollo Ecologico y Rural** in Mexico City (COCODER) to volcano rabbit areas is minimal. **Wardening** of the Izta-Popo National Park and in the Special Protected Zones to the south of Mexico City (Volcan el Pelado and Volcan Tlaloc) is necessary. Although actions to frustrate hunting must be enforced, ways of making rational exploitation of natural resources compatible with wildlife protection must be identified. Controlled burning at regulated densities can be made compatible with the recovery of other areas and the conservation of wildlife.
3. Education campaigns at village, national and international levels must be started. Public awareness of the species' habitat is essential. Information on the impact of land use methods incompatible with sustained development and conservation should be made available to villages adjacent to the core habitats. Most local inhabitants are unaware of the protected status of the species.
4. The value of captive colonies at Mexico City and Jersey Zoos to create and foster public awareness cannot be underestimated. Under no circumstances should the species be introduced as a laboratory animal as suggested by some authors (Granados, 1981), since this could create a demand that could eventually imperil the wild populations.



Volcano rabbit habitat in the Ajusoo Range
(Photo by Diana Bell)

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Chapter 13: Exotic Populations

John E.C. Flux, A.G. Duthie, T.J. Robinson and J.A. Chapman

Australia and New Zealand

No lagomorphs are native to Australia or New Zealand, but Australia did have marsupial equivalents of rabbits and hares in the rabbit-eared bandicoot or bilby *Macrotis lagotis* and hare-wallabies *Lagorchestes*, *Lagostrophus*. Both countries were settled by Europeans in the early 19th century, and soon set up acclimatization societies to import and liberate “desirable” game, fish and songbirds. Similar societies existed in many countries, including Britain, France, Italy, Burma, India and China, so exchanges were easily arranged. Their aim, in the words of the 1882 report of the acclimatization society for Victoria, was “to enrich it by stocking its broad territory with the choicest products of the animal kingdom borrowed from every temperate region on the face of the globe.” These societies were well funded and efficiently organized, so it is perhaps surprising that only two lagomorphs, the brown hare *Lepus europaeus* and the European rabbit *Oryctolagus cuniculus* were successfully introduced. An offer of £2.10 each for the first 20 Indian hares delivered, “extensively circulated in the principal shipping ports of the world” by the Victorian society in 1863, was luckily unclaimed.

The pattern of introduction was similar in both Australia and New Zealand, probably because there was much interchange of people and ideas, and both adopted sheep farming as the dominant land use. Domestic rabbits had arrived by 1788, taken out for food by the earliest settlers, and some had escaped and were living around the villages by about 1820-1840. These did not spread, perhaps because the land was not sufficiently developed and feral domestic rabbits fell easy prey to native carnivores, cats and dogs (Rolls 1969). Wild-type rabbits from England were then introduced, at Geelong in Australia in 1859 and in Southland, New Zealand, in 1862 (Wodzicki 1950). Silver-grey domestic rabbits, a favored breed for furs, were liberated at Kaikoura and Nelson, New Zealand, in 1865 and spread far inland; but they were no match for the wild-type rabbits which overtook them from the south (Thomson 1922). Within ten years rabbits were causing extensive damage to farms and the first Rabbit Nuisance Act was passed in New Zealand in 1876. Tasmania had its first anti-rabbit legislation in 1871, South Australia in 1875, Victoria in 1878 and New South Wales and Queensland followed in 1880.

Rabbits spread to occupy the southern half of Australia (4 million km²) in 60 years. Early rates of spread were phenomenal, averaging 125km/year across the south and up to 350km/year in north Australia (Myers 1971, Strong 1983). Even now the distribution (Fig. 13.1) is not stable and the rabbit “continues to probe Australian habitats and is presently making a

slow advance northwards along the cool highlands into tropical Queensland” (Myers 1983). In arid regions rabbits occupy watercourses, expanding into surrounding country in occasional wet years. Those in subalpine areas are restricted to open grassy valleys. The land between these extremes, converted to sheep farms, provided rabbits with ideal conditions.

The damage caused by rabbits in Australia is legendary. “They bred in thousands of millions and died in thousands of millions: by diseases, natural and introduced; by drought and flood; by all manner of traps, poisons, fumigants, and enemies natural and introduced; but they thrived and they thrive yet” (Rolls 1969). The most spectacular scenes of abundance, such as rabbits piled up a metre deep against a boundary fence, or drinking shoulder to shoulder round a small pool, were part of the initial explosive phase. Numbers soon declined, to stabilize at the 20-100/ha level of a high rabbit population.

Even these densities, of course, cause enormous financial loss to farmers, but there are few accurate measurements. The best figures, collected by Fennessy (1966) showed increases in stock numbers of 26-100% in South Australia and New South Wales following the sudden removal of rabbits in

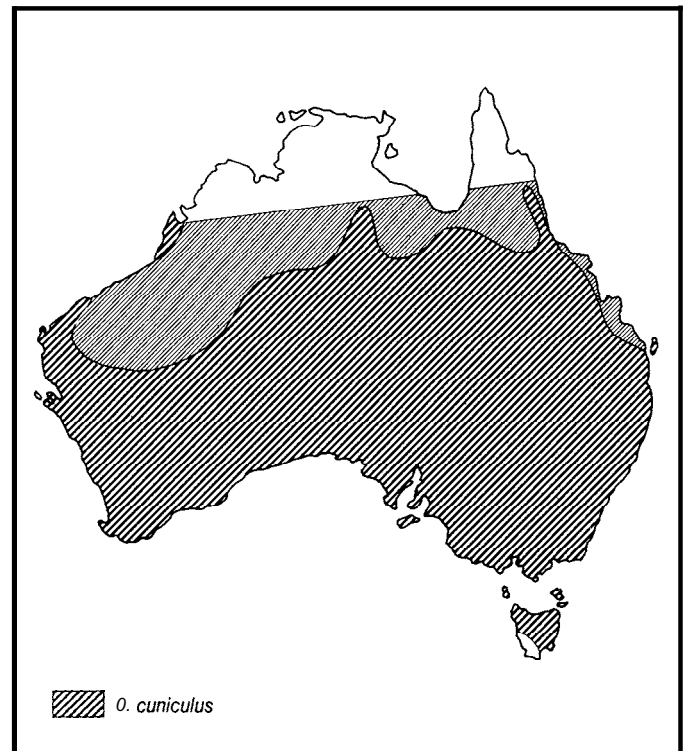
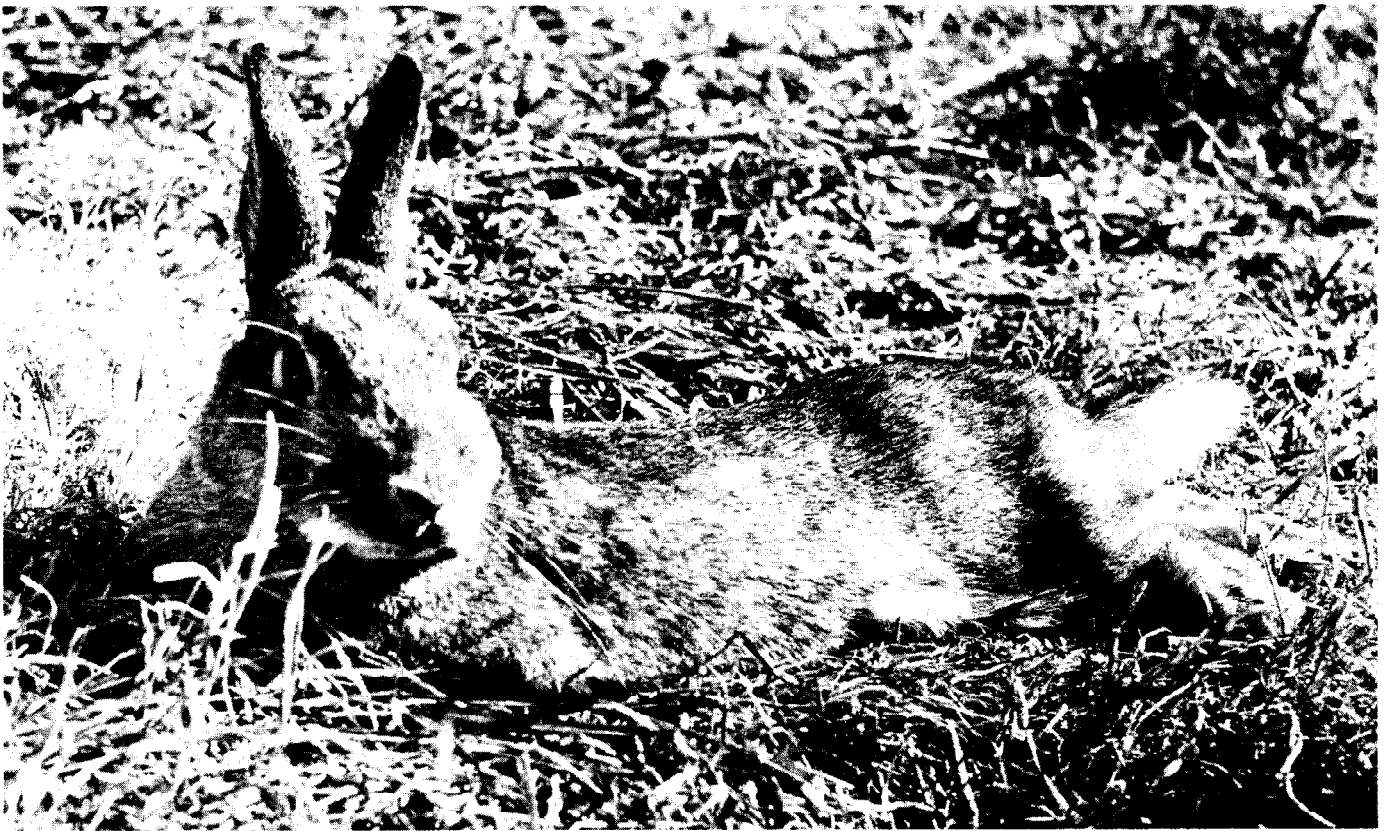


Figure 13.1. Distribution of the European rabbit *Oryctolagus cuniculus* in Australia. The area in lighter tone may be occupied in years of favorable rainfall. (From Myers 1983).



The European rabbit *Oryctolagus cuniculus* (Photo by R L. Edgar)

the 1950s. After myxomatosis, it was calculated from the increased wool and meat production that rabbits had caused £34 million worth of damage a year, while the sale of rabbit skins and carcasses fetched only £10 million in 1951-52. To put these figures in perspective, a careful assessment of rabbit damage costs to wheat, field crops and grassland in Britain in the 1950s before myxomatosis was £40-50 million a year, offset by £15 million from the sale of rabbit meat and furs. In New Zealand, Wodzicki (1950) estimated rabbit damage in terms of reduced sheep-carrying capacity to be 3.5-4 million in 1945, compared with income of £1.3 million from rabbit exports. Although apparently more severe in Britain, the problem in Australia and New Zealand was more significant because of their dependence on farming.

Faced with a problem of such economic importance, Australians tried everything. Enormous fences were built: 346 miles long between New South Wales and South Australia; 700 miles between NSW and Queensland; and 1139 miles on the border of West Australia, followed by another of 700 miles when rabbits crossed the first line. Individual fields were fenced and rabbits eradicated by poisoning, trapping, shooting, digging, ferreting and gassing, all of which provided only temporary relief. Before the introduction of myxomatosis in 1950, Myers (1971) measured rabbit density at four study areas in Victoria and New South Wales at 44, 59, 190 and 412 rabbits/ha. In 1970, after myxomatosis, these had become 2.9; 0.3, 0.6 and 0.9 rabbits/ha, respectively. Overall, Myers con-

cluded that rabbit numbers in 1970 were "clearly less than 1% of their 1950 levels." Predators now exerted significant control, aided by poisoning in problem areas. Eruptions still occur after good rainfall and grass production, but the average populations now seem to be 10-20% of the pre-myxomatosis levels, rising slowly as rabbits and the virus co-evolve.

In New Zealand, the initial explosion of rabbit numbers was as severe as in Australia, especially in the South Island and eastern North Island. The same wide range of control methods was tried, including hundreds of miles of rabbit fencing, with the same lack of success. In addition, New Zealand attempted biological control by introducing many thousands of stoats *Mustela erminea* weasels *M. nivalis* and ferrets *M. furo* despite strong objections from acclimatization societies and scientists (Martin 1885). These predators did not control the rabbits but adversely affected native fauna, naive to mammalian predation. By 1900 rabbit numbers had peaked in the South Island, but the range was still spreading in the North Island (Wodzicki 1950). From 1900 to 1945 an average of 12 million rabbits was exported each year, with extremes between six and twenty million. Because rabbits were completely out of control over most of New Zealand following World War II, the Rabbit Nuisance Amendment Act was passed in 1947. This established a Rabbit Destruction Council and led to the "killer policy," total decommercialisation of rabbits and a most efficient national organization. By aerial and ground poisoning with 1080 in carrot and jam baits,

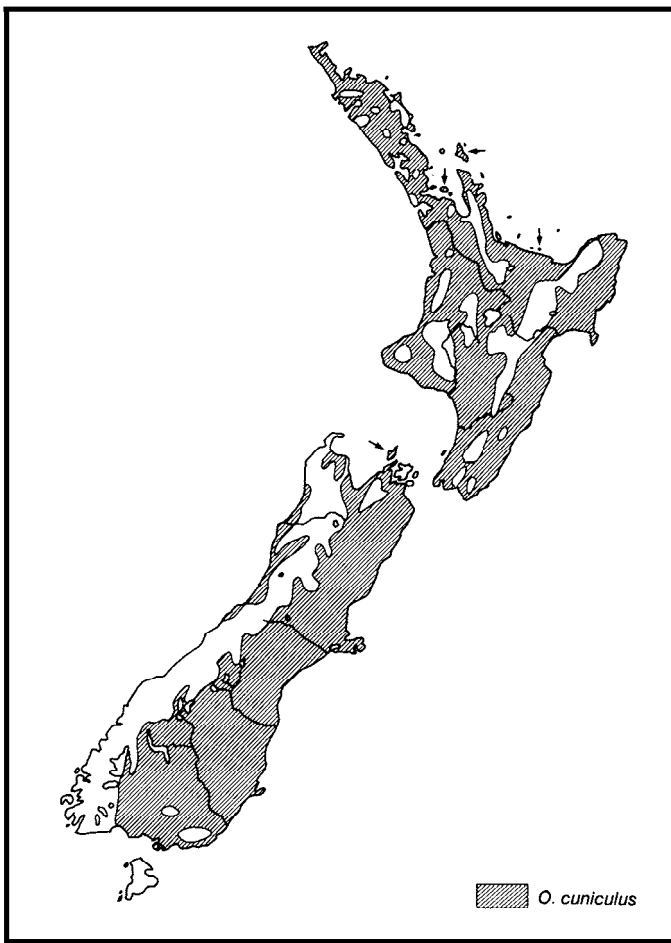


Figure 13.2. Distribution of the European rabbit *Oryctolagus cuniculus* in New Zealand.

followed up with gun and dog, or spotlight shooting at night, rabbit populations were reduced by over 90% (Bull 1956, Howard 1958). Overgrazing by stock contributes to the rabbit problem and rabbits dislike long, wet grass; it is often said in New Zealand that top-dressing with superphosphate killed more rabbits than 1080. An official attempt to introduce myxomatosis in the early 1950s failed (Filmer 1953) and the continuing absence of the disease in New Zealand may in fact allow rabbits to be kept at lower numbers than in Australia and Britain (Gibb and Flux 1983).

Rabbits still exist on open grassland throughout New Zealand below about 1,000m altitude (Fig. 13.2). Densities are, however, exceptionally low compared with other countries; perhaps one rabbit per 10-20ha. At these densities, cats, stoats and ferrets keep numbers stable, and the removal of annual control by Pest Destruction Boards from two million hectares has not led to a resurgence of rabbits (Gibb et al. 1969, Williams 1983). In Central Otago, the Mackenzie Country and Marlborough, however, some farms still have serious rabbit problems with densities of about 20-40 rabbits/ha. These areas have a severe winter which shortens the rabbit breeding season, and in the absence of young rabbits and

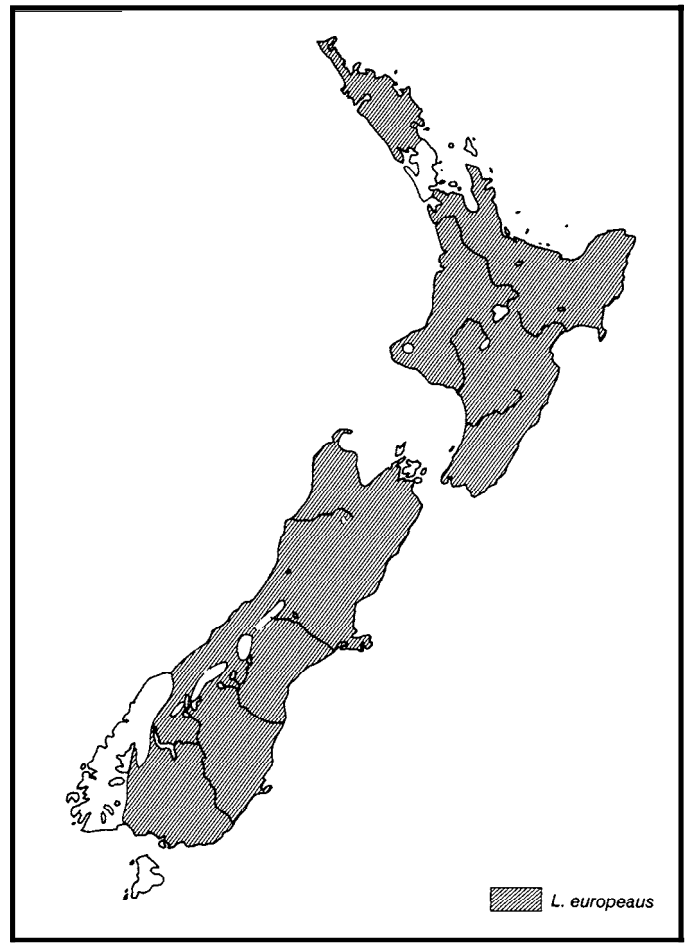


Figure 13.3. Distribution of the European hare *Lepus europaeus* in New Zealand.

sufficient alternative prey, too few predators may be able to survive (Dr. B.M. Fitzgerald, pers. comm.). Although raising domestic rabbits has been legal since 1980, wild rabbits cannot be traded; hence there is little benefit gained from rabbits in New Zealand apart from sport shooting by youngsters.

The first European or brown hares were introduced into New Zealand in 1851 for sport (Donne 1924), but this liberation may have been unsuccessful. In the next 20 years a few dozen animals were brought in, chiefly from England via Phillip Island in Australia, and by the 1880s shooting restrictions on hares were lifted in Canterbury. Hares spread more rapidly than rabbits, to occupy the whole of New Zealand apart from forested areas, except for Fiordland, part of Northland and land over 2,000m altitude (Fig. 13.3). Until 1966 about 40,000 hares a year were exported to Europe, but the damage to forestry and orchards, and competition with domestic stock for grazing probably balanced the benefits.

Unlike rabbits, European hares appear to control their own density, and even on islands without predators do not exceed 3.4 hares/ha (Abildgard et al. 1972). Densities almost as high (2-3/ha) are recorded in inland Canterbury (Parkes 1984), but over most of the country the average would be one

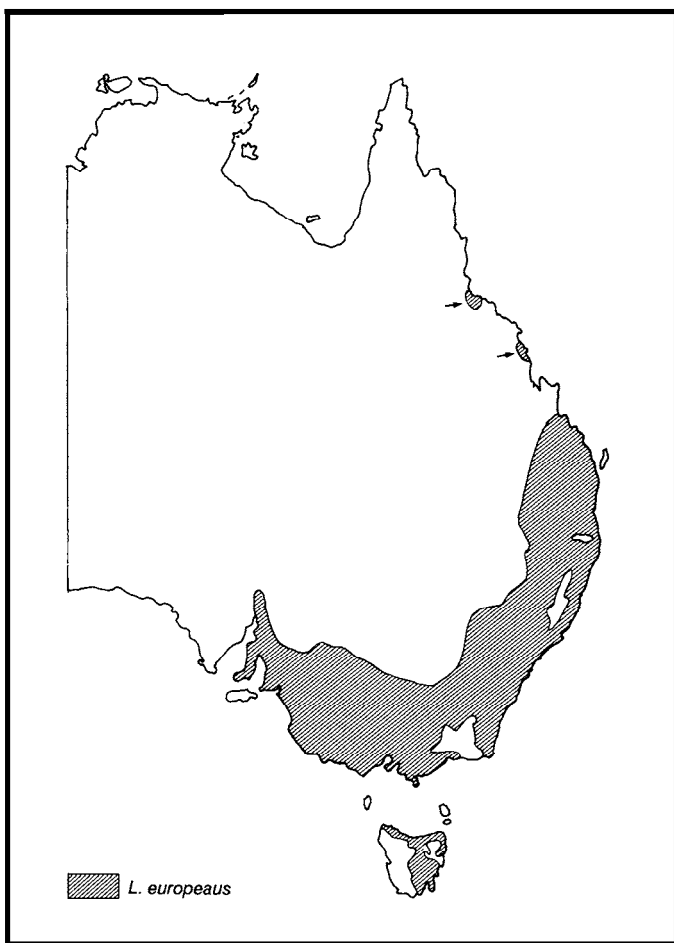


Figure 13A. Distribution of the European hare *Lepus europaeus* in Australia (From Jarman 1986).

hare to 10-20ha (Flux 1981). They are regarded as a minor pest and not favored for food or sport, although in the absence of foxes some are used as quarry by hunters on horseback. In color, behavior and reproduction, hares are similar to their British stock (Flux 1967a). The most noticeable difference is that hares occupy alpine grassland above the timberline, the habitat of the mountain hare *Lepus timidus* in Europe. Numbers at high altitudes are low (Flux 1967b) but damage to slow-growing native vegetation can be significant, especially in National Parks. Interestingly, these alpine hares exist on an entirely novel flora. Unlike Australia, New Zealand has no native carnivores that benefit from the presence of either hares or rabbits.

In Australia, three pairs of hares from Britain placed on Phillip Island increased to 200 by 1865 and numbers were then liberated in several places. They spread across New South Wales at 60km/year, mainly along the Dividing Range (Jarman 1986). After arrival in a district, hares increased for 10-20 years before declining, and bounties paid on hare scalps in the Armidale region, NSW, show this pattern. Bounty payments also show pronounced summer peaks during the period of increase and more even distribution over the year in the decline, which Jarman (1986) suggested could reflect reduced

ability of the vegetation to support early summer recruitment; but it seems equally likely that casual hunters killed more hares in summer in years when they were plentiful. Some idea of their abundance is given by Jarman (1986): "Between 1890 and 1902 bounties in New South Wales were paid on a minimum of three to four hundred thousand hare scalps annually." Hares spread ahead of the rabbits in the early years, and their subsequent decline was often attributed to the arrival of rabbits, which dominate European hares; rabbits also graze more closely and carry parasites to which hares are susceptible. Although they are still spreading slowly as land is cleared for farming, the distribution has remained almost unchanged for 70 years (Fig. 13.4).

The limited distribution of hares in Australia is remarkable. In other countries where European rabbits and hares co-exist, including Sweden, Russia, Italy, North and South America and New Zealand, hares occupy far more of the country than do rabbits. Ireland is an exception, but European hares there face competition with the mountain hare. The relative success of hares is generally explained by their greater range of climatic and habitat tolerance, but this apparently does not apply to Australia. One possible explanation is that hares start breeding in mid winter, regardless of the climate, while rabbits are opportunistic breeders, taking advantage of green vegetation following sporadic rains (Flux 1965), a dominant feature in inland Australia. Their distribution does not match any obvious vegetation boundary, but Jarman (1986) points out that it coincides with areas having a moisture index that allows plant growth in winter. Hares in Australia, however, breed for almost nine months of the year (Hesterman and Kogon 1963), so it is still curious that lack of winter breeding should limit their geographical distribution.

To summarize, rabbits in Australia are still widespread and probably increasing slowly in abundance and distribution; severe damage is now local and sporadic, varying as the population increases during wet years or declines following outbreaks of myxomatosis. In New Zealand, rabbit control without myxomatosis has been highly efficient and over 95% of the country populations are stable at very low levels, apparently kept there at no cost by predators. There are three South Island areas where rabbit populations remain intractable. Hares are stable in distribution and numbers in both countries, at similar population levels, causing some damage to trees and crops. They are probably the least troublesome of any of the introduced mammals.

Africa

The natural range of the European rabbit in Africa is confined to the coastal regions of Morocco and Algeria (Petter 1972). Feral populations are reportedly found in lower Egypt (Petter 1972) as well as on certain South African offshore islands. The introduction of the European rabbit to southern Africa began shortly after the establishment of a settlement at the Cape by the Dutch in 1652. An excellent account of the initial and sub-

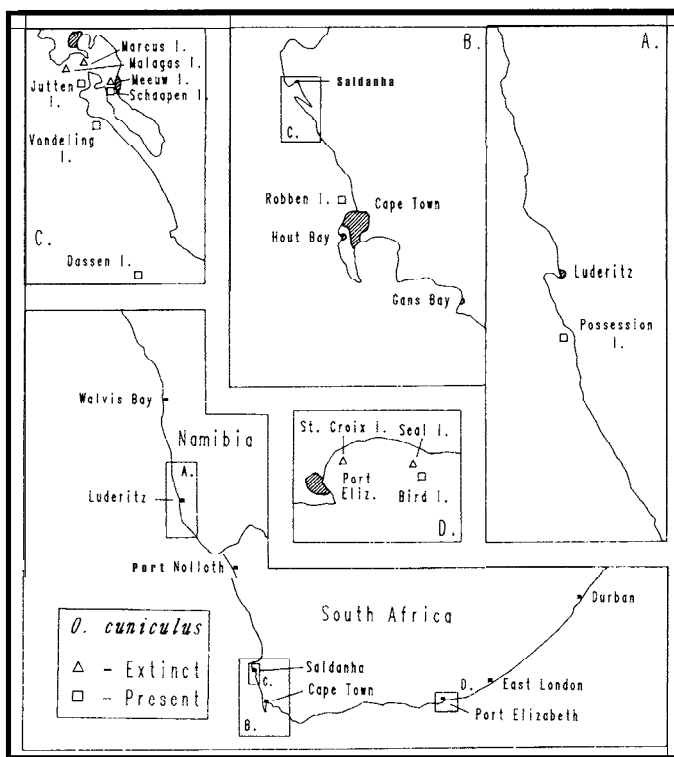


Figure 13.5. Distribution of the European rabbit *Oryctolagus cuniculus* on islands off South Africa

sequent introductions is given in Smithers (1983) which forms the basis of this report. The impetus for attempts to establish the species in South Africa was to provide a ready source of fresh meat for both the garrison stationed at the Cape and passing ships. Interestingly however, the early releases of rabbits took place on surrounding offshore islands and not on the mainland, apparently in accordance with instructions received from the Dutch East India company "...according to your order we keep none here on the continent less they damage the gardens and crops (Leibbrandt 2: 1900 in Smithers 1983).

Rabbits were first released in 1654 on **Robben Island**, but failed to thrive. Two subsequent releases on this island in 1656 and 1658 were necessary before the population was established and by 1659 they were reported to be abundant (Thorn 1958 in Smithers 1983). Introductions to other offshore islands were also undertaken. In total, European rabbit populations were established at 12 such islands at one time or the other although Smithers reports four of these no longer support rabbits (Fig. 13.5).

Accidental or deliberate introductions of the species on the mainland have undoubtedly occurred in the recent and historic past. However, as far as is known, none of these other than in Egypt has been successful. The inability of the species to establish itself, as it has done so successfully, for example, in Australia and New Zealand, is probably due to the predation pressure on the African Continent (Smithers 1983).



Figure 13.6. Distribution of the European rabbit *Oryctolagus cuniculus* in South America (from Chapman and Johnson, in press)

North, Central and South America

The European rabbit and the European hare have been widely introduced throughout the New World. The most successful introductions have been in South America, where Argentina and Chile have extensive populations of both species. Small populations of both species are also found in the United States and Canada. A detailed account of the distribution and status of exotic Leporidae in South America is presented in Chapman and Johnson, in press (see Figs. 13.6 and 13.7). Dean and De Vos (1965) discuss the distribution of the European hare in North America. A map of the distribution of the European rabbit worldwide is available in Flux and Fullagar (1983).

In North and Central America, European rabbits and hares have not spread widely, if at all, probably because of the presence of native predators and competitors. In South America, however, the European hare now occupies most of the continent south of latitude 30°S. The European rabbit has spread throughout Chile from 28°S and is now rapidly invading Argentina despite the introduction of myxomatosis. Apart



Figure 13.7 Distribution of the European hare *Lepus europaeus* in South America (from Chapman and Johnson, in press)

from economic damage to crops and pasture, one serious consequence seems to be a decline in the numbers of indigenous rodents occupying the same ecological niche, such as the Patagonian maras (*Dolichotis* spp.). The eastern cottontail *Sylvilagus floridanus* has also been widely translocated in North America and is established in Oregon and Washington (Fig. 5.5).

Europe

There have been numerous attempts to introduce various species of cottontails *Sylvilagus* and North American hares *Lepus* into Europe, particularly Italy and France. Attempts to establish North American jackrabbits have apparently failed. However, there is considerable concern about eastern cottontail *S. floridanus* and New England cottontail *S. transitionalis* introduction attempts. These introduction attempts have been in an effort to establish alternate game species for native rabbits and hares in the region (see Sasse 1983).

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Cottontails *Sylvilagus* spp. have not been successfully introduced into Europe, despite repeated attempts (Photo by K. B. Fuller)

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Chapter 14: Conservation Action Needed for Rabbits, Hares and Pikas

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Introduction

The data presented in the previous chapters constitute the most thorough overview ever made of the lagomorphs from a conservation perspective. In this section, the data are used to compile a list of actions needed to conserve and manage lagomorphs more effectively. These actions are divided into the following categories:

- Management Guidelines for Common Species;
- Conservation of Globally Threatened Species;
- Conservation of Other Species of Concern;
- Priorities for Conservation-Related Research on Lagomorphs.

This chapter does not attempt to go into great detail on the various conservation issues, and the reader is referred to relevant sections of earlier chapters for more information.

Management Guidelines for Common Species

Many parts of the world support some common lagomorph species. Often these are of considerable economic importance, either for the fur trade, or more usually as game species. These uses of lagomorphs can frequently be compatible with their conservation, provided that certain basic management procedures are adopted. In general, these can be summarised as follows:

Hunting

In many cases, the hunting of lagomorphs has been sustainable through luck rather than management design. In some cases, most notably the brown hare *Lepus europaeus* in Europe, hunting levels are no longer sustainable and need to be

reduced. Throughout Europe, thorough population studies of the species need to be carried out and hunting quotas then set and enforced, that allow populations to recover. The long-term aim should be for each European country to set annual quotas based on regular monitoring of the populations.

Habitat Management

Recent changes in agricultural practices in Europe (including the use of fertilizers and pesticides, and the planting of huge fields of monoculture crops) have resulted in declines in the European hare population. This is part of the wider problem of decisions taken to increase the productivity of agriculture, without due consideration being given to other forms of land use, such as the management of game species. Land use planning programs should adopt a broader approach in future and should include environmental considerations. Land use decisions should be made on a cross-sectoral basis which takes into consideration the impact on other sectors (i.e. nature conservation, sport hunting, the fur industry, etc.). It should be realised that intensive agriculture is often the most profitable form of land use only because of the hidden government subsidies that it receives; its intrinsic profitability is frequently less than often assumed.

Introductions

In a number of places, lagomorphs have been introduced to areas outside their natural distribution, often in an attempt to supplement the existing range of game species. This practice should be opposed vigorously. Such introductions can severely disrupt the natural ecological balance and threaten native species. The proposed introductions of cottontails *Sylvilagus* into parts of western Europe are likely to be especially damaging and should be prevented. The IUCN/SSC Lagomorph Specialist Group Statement on the Introduction of Exotic Lagomorphs is included in Appendix 1 and is compatible with the 1987 IUCN Position Statement on Translocations of Living Organisms.

Table 14.1 The globally threatened lagomorph species

Species	IUCN Category of Threat	Countries of Occurrence
Gaoligong Pika <i>Ochotona gaoligongensis</i>	Indeterminate	China
Ili Pika <i>Ochotona iliensis</i>	Indeterminate	China
Koslov's Pika <i>Ochotona koslowi</i>	Vulnerable	China
Muli Pika <i>Ochotona muliensis</i>	Indeterminate	China
Nubra Pika <i>Ochotona nubrica</i>	Indeterminate	China, India, Nepal
Thomas' Pika <i>Ochotona thomasi</i>	Indeterminate	China
Tehuantepec Jackrabbit <i>Lepus flavigularis</i>	Endangered	Mexico
Black Jackrabbit <i>Lepus insularis</i>	Rare	Mexico
Tres Marias Rabbit <i>Sylvilagus graysoni</i>	Endangered	Mexico
Omiltemi Rabbit <i>Sylvilagus insonus</i>	Endangered	Mexico
San Jose Brush Rabbit <i>Sylvilagus mansuetus</i>	Indeterminate	Mexico
Pygmy Rabbit <i>Brachylagus idahoensis</i>	Vulnerable	United States
Riverine Rabbit <i>Bunolagus monticularis</i>	Endangered	South Africa
Hispid Hare <i>Caprolagus hispidus</i>	Endangered	India, Nepal
Sumatran Rabbit <i>Nesolagus netscheri</i>	Indeterminate	Indonesia
Amami Rabbit <i>Pentalagus furnessi</i>	Endangered	Japan
Volcano Rabbit <i>Romerolagus diazi</i>	Endangered	Mexico

Conservation of Globally Threatened Species

Some 17 species of lagomorph are now considered to be globally threatened, as documented in Table 14.1; the conservation actions needed for each of these 17 species are listed below on a country-by-country basis.

China

Six species of globally threatened lagomorph occur in China, all of them pikas. In nearly every case they are still too poorly known for it to be possible to make detailed conservation recommendations.

Gaoligong Pika *Ochotona gaoligongensis*

This recently described species is known only from Mount Gaoligong, Yunnan Province, China. Nothing is known of its status.

The following priority activities have been identified for the conservation of this species:

- 1. Research.** The systematic status of this species needs to be resolved, since it is possible that it is closely related to Forrest's pika *O. forresti*. This would require the collection of additional specimens and careful comparison with related species.
- 2. Status Surveys.** A survey should be carried out to assess the status and conservation requirements of this species on Mount Gaoligong.
- 3. Conservation Action.** Based on the results of the research and surveys outlined above, appropriate conservation measures should be introduced in the Mount Gaoligong area.

Ili Pika *Ochotona iliensis*

This recently described species is known only from Borohoro Shan area, Xinjiang Province, China. Nothing is known of its status.

The following priority activities have been identified for the conservation of this species:

- 1. Research.** The systematic status of this species needs to be resolved, since it is possible that it is closely related to the red-eared pika *O. erythrotis* or the Turkestan red pika *O. rutila*. This would require the collection of additional specimens and careful comparison with related species. Research should also focus on the postulated decline of this species due to global warming.

Biological Control

The deliberate use of any disease or predator to control lagomorph populations should only be permitted after stringent conditions have been met, as outlined in the IUCN/SSC Lagomorph Specialist Group Statement on the Biological Control of Lagomorphs (see Appendix 1) .

2. **Status Surveys.** A survey should be carried out to assess the status and conservation requirements of this species in the Borohoro Shan area.
3. **Conservation Action.** Based on the results of the research and surveys outlined above, appropriate conservation measures should be introduced in the Borohoro Shan area.

Kozlov's Pika *Ochotona koslowi*

This highly distinctive pika is only known from the Arkatag Range, a spur of the Kunlun Mountains west of the junction of Xinjiang, Xizang and Qinghai Provinces in China. It is believed to be threatened.

The following priority activities have been identified for the conservation of this species:

1. **Status Survey.** A thorough survey is needed to assess the status and conservation requirements of this very restricted species. The survey should produce clear recommendations for the conservation of the species and its habitat.
2. **Conservation Action.** Based on the results of the above-mentioned survey, a conservation initiative should be launched in the Arkatag Range. The habitats of this area are already known to be severely impacted, so some form of improved management will almost certainly be necessary.
3. **Research.** The possible impact of vertebrate control campaigns on populations of this species should be investigated and the results used to help design the integrated conservation program.

Muli Pika *Ochotona muliensis*

This very rare species is known only from thickets and steppes in western Sichuan Province, China. There have been no records in the last 25 years and it could be seriously threatened.

The following priority activities have been identified for the conservation of this species:

1. **Research.** The systematic status of this species needs to be resolved, since it is possible that it is closely related to the Glover's pika *O. gloveri*. This would require the collection of a limited number of additional specimens and careful comparison with related species. Research should also focus on the impact of vertebrate control programmes on

the Muli pika, since it is possible that the resulting chemical contamination has severely threatened this species.

2. **Status Surveys.** A survey should be carried out to assess the status and conservation requirements of this species in western Sichuan Province.
3. **Conservation Action.** Based on the results of the research and surveys outlined above, appropriate conservation measures should be introduced in western Sichuan Province.

Nubra Pika *Ochotona nubrica*

This enigmatic species occurs in a narrow range along the southern Tibetan plateau, as well as in neighbouring India and Nepal. It is very poorly known.

The following priority activities have been identified for the conservation of this species:

1. **Status Surveys.** A survey should be carried out to assess the status and conservation requirements of this species along the southern Tibetan plateau, with a view to making conservation recommendations. The ecological requirements of the species are not understood at all.
2. **Conservation Action.** Based on the results of the surveys outlined above, appropriate conservation measures should be introduced in the southern Tibetan plateau area.

Thomas' Pika *Ochotona thomasi*

This species is known only from isolated mountain ranges in Gansu, Qinghai and Sichuan Provinces, China. It is rare and may be threatened.

The following priority activities have been identified for the conservation of this species:

1. **Research.** Research should focus on the impact of vertebrate control programmes on this species, since it is possible that the resulting chemical contamination has severely threatened Thomas' pika.
2. **Status Surveys.** A survey should be carried out to assess the status and conservation requirements of this species in Gansu, Qinghai and Sichuan Provinces.
3. **Conservation Action.** Appropriate conservation measures should be introduced, based on the results of the research and surveys outlined above.

India

Two globally threatened lagomorph species occur in India.

Nubra Pika *Ochotona nubrica*

This enigmatic species occurs in a narrow range in the Ladak Range, as well as in neighbouring China and Nepal. It is very little known.

The following priority activities have been identified for the conservation of this species:

1. **Status Surveys.** A survey should be carried out to assess the status and conservation requirements of this species in the Ladak Range, with a view to making conservation recommendations. The ecological requirements of the species are not understood at all.
2. **Conservation Action.** Based on the results of the surveys outlined above, appropriate conservation measures should be introduced in the Ladak Range.

Hispid Hare *Caprolagus hispidus*

This species is seriously endangered, surviving in a few isolated pockets across the former range of its tall grassland habitat in northern India and southern Nepal. It is threatened by habitat destruction for agriculture, forestry, human settlement, flood control and irrigation schemes, together with the adverse effects of dry season burning, overgrazing and harvesting of remaining tall grasslands.

The following priority activities have been identified to ensure the survival of this species:

1. **Maintenance of Protected Areas.** The continued survival of this species in India depends upon the maintenance of the tall grass habitat in the following protected areas (note that the species also occurs in Nepal: see that account): Manas Reserve Forest, Manas Sanctuary, Manas Tiger Reserve, Barnadi Reserve Forest, Ripu Reserve Forest, Subankhata Reserve Forest, Orang Wildlife Sanctuary, Jaldapara Wildlife sanctuary, Buxa Tiger Reserve, Valmiki Wildlife Sanctuary, Dudwa National Park and possibly Kanha National Park. It should be noted that governmental authority over some of the reserves in Assam is now weak, especially the Manas complex, as a result of security problems. In some other reserves there is heavy overgrazing by cattle, notably the Buxa Tiger Reserve, and this needs to be brought under control. It is of great importance that control of these reserves be regained, but also that in future the management plans of these areas are designed to ensure that the local Bodo people derive tangible economic benefits from the existence of the reserves. This might take the form of appropriate buffer-

zone developments, especially around the very important Manas complex of reserves.

2. **Improvement of Habitat Management.** The immediate threats to the relict populations of the hispid hare should be alleviated by a change in reserve management practices, from uncontrolled dry season burning of its tall grassland habitat to a system of carefully controlled rotational burning such that large areas of suitable habitat (i.e. providing optimal cover, food resources, etc.) are available throughout the year. The detailed formulation of appropriate long-term management plans for these remnant areas of tall grassland should draw on the results of the research programs recommended below.
3. **Status Surveys.** Status surveys are needed in a number of areas that have not previously been investigated for this species. These include several areas of north-eastern India. Faecal evidence of the hispid hare occurring in Kanha National Park requires confirmation, since this site is some distance south of the present known range of the species and would indicate the need for additional surveys for hispids in remaining grassland patches between these two areas.
4. **Research. 1: Long-term research programs** examining the effects of each of the several disturbance factors (e.g. burning, thatch harvesting and grazing) operating on hispid hare habitat are required to formulate appropriate long-term management plans for the remnants of tall grassland habitat. Research into burning, for example, should investigate the effects of factors such as timing, frequency and soil water content on both the vegetation and the hare populations so that optimum management plans can be developed for individual areas.
2: Long-term studies of the behavioral ecology and reproductive biology of the hispid hare are urgently required, concentrating on habitat requirements, breeding biology and home range use throughout the year (so far only studied in the early dry season). It is important that these studies include the monsoon period, when the marshy areas used as refugia during the early dry season post-burn period are likely to be among the first areas to become inundated.
5. **Captive Breeding.** A captive breeding program for this species needs to be initiated to provide a nucleus of animals for reintroduction into the wild, should this become necessary. At least 30 animals should be used to form the founder captive stock to avoid inbreeding problems.

Indonesia

Of the two lagomorph species that occur in Indonesia, only one is of conservation concern.

Sumatran Rabbit *Nesolagus netscheri*

The Sumatran rabbit is an endemic genus restricted to the montane forests of western Sumatra. There is a great scientific interest in the species because it is considered to be a primitive relict form, because of its unusual striped coloring and because it is one of the very few lagomorphs which lives in thick equatorial forest. In addition, there is possible commercial interest in domesticating this animal for use in tropical countries where the European rabbit *Oryctolagus cuniculus* is not so well adapted.

The following priority activities have been identified for the conservation of this species:

1. **Status Surveys.** The status of the Sumatran rabbit remains almost completely unknown. It seems to have a very low population density and is probably restricted to inaccessible montane forest. It may have a requirement for rich volcanic soils, further limiting its distribution, and this needs to be investigated. The highest priority for this species is to locate it in the wild through a thorough status survey of all the locations in which it has been reported in the past, and to assess its conservation requirements.
2. **Habitat Conservation.** Montane forest in Sumatra is now being cleared rapidly, through a combination of felling of timber, planting of vegetables and settling of immigrants from Java through the transmigration program. It is against this background that a new National Park is proposed for Mt. Kerinci-Seblat. It is of the utmost importance that this park be formally gazetted and measures taken to ensure the survival of the full range of habitats and species within it. The survey referred to above will need to determine whether the park contains a viable population of the Sumatran rabbit. It is essential that a management plan be developed for the new park allowing for appropriate forms of buffer-zone development in the surrounding area, to increase the standard of living of the local communities without jeopardizing important conservation priorities (possibly through the new WWF-funded project there). The same considerations also apply to the existing Gunung Leuser and Barisan-Selatan National Parks, where the species probably occurs.
3. **Research.** Once a population of this elusive species has been found, it will be necessary to carry out detailed studies on its habitat requirements. A greater knowledge of the signs left by these animals will enable surveys of other areas to proceed more rapidly. Scientific studies should also be geared towards developing habitat management guidelines for the species, to be incorporated in the management plans of reserves within its range.

4. **Captive Breeding.** If a population can be located, it is important to invest in a captive breeding program for the species to provide a nucleus of animals for reintroduction, should this be necessary.

Japan

The Amami rabbit is the only Lagomorph occurring in Japan that is of international conservation concern.

Amami Rabbit *Pentalagus furnessi*

The Amami rabbit is an endangered species found only on Japan's Amami Island and Tokuno-shima, part of the Ryukyu Island chain. These islands have many endemic terrestrial vertebrate species and subspecies. Amami Island is very important for endemic species conservation and the Amami Rabbit is a representative of the unique biocommunity of the island.

The following priority activities have been identified to ensure the survival of this species:

1. **Habitat Conservation and Management.** To enable this species to survive, a habitat mosaic of mature oak forests and young second-growth stands is required. This enables the Amami rabbit to obtain important food supplies throughout the year. In order to maintain this mosaic, careful habitat management is necessary; certain forests should be set aside to become mature, since such old forests are now greatly reduced in area.
2. **Control of Introduced Species.** The Amami rabbit suffers greatly from introduced predators such as feral dogs, feral cats and mongooses. As a result, the species tends to be absent from areas near human settlements. Populations of introduced predators should be controlled in important areas for the species.
3. **Research and Monitoring Programs.** A few research programs have been conducted, sponsored by the central government, focusing on population estimates, food habits and nest site selection of the Amami rabbit. These, however, are not sufficient to monitor the population because the studies are too infrequent and the amount of information collected during each period is too small. An ongoing budget is required for a research or a monitoring program with the aim of assessing conservation and management needs for the species. Researchers willing to carry out such long-term research programs also need to be identified.

Mexico

With six species of threatened lagomorph, Mexico (together with China) is the highest priority country in the world for the conservation of these species.

Tehuantepec Jackrabbit *Lepus flavigularis*

The Tehuantepec jackrabbit is the most endangered hare in North America. Its geographic range is restricted to a small area in Oaxaca and Chiapas in Mexico. Its historic geographic range has been reduced; unfortunately no information is available about its present distribution and population numbers.

The following priority activities have been identified to ensure the survival of this species:

1. **Habitat Conservation and Management.** The populations of the Tehuantepec jackrabbit have been depleted by habitat destruction. The species is restricted to riparian vegetation, sand dunes and shrub forest, which never exceeds a 4-5km wide strip along the shores of salt water lagoons on the northern side of the Gulf of Tehuantepec. Its habitat is threatened by expanding agriculture to support the growing local human population. The only real chance of saving this species is to establish reserves for it in areas identified as supporting the denser populations. Reserve sites should be identified by the surveys referred to below and planned to ensure that their establishment does not cause conflicts with local communities.
2. **Regulation of Hunting.** The Tehuantepec jackrabbit is also suffering from hunting. It is important to ensure an effective ban on the hunting of the larger populations which have a chance of long term viability, as part of the management programs for the new reserves referred to above.
3. **Education Program.** Education programs are needed to inform the local communities of the uniqueness of this species and the value of its preservation. These programs should include advice to the local people on forms of land use that are both beneficial to them and which are likely to be sustainable in the long term.
4. **Status Surveys.** Surveys are required to provide accurate inventories and documentation on the distribution of the species, with a view to identifying potential reserve sites and assessing its habitat requirements.
5. **Research.** The biology of the Tehuantepec jackrabbit is unknown. The only information available concerns its systematics. Research on basic biology is clearly needed. It is important to document its habitat preferences and the effect of grazing and other types of habitat disturbance on the populations of this species.

6. **Captive Breeding.** A captive breeding programme should be established to enable reintroduction in the event of extinction in the wild.

Black Jackrabbit *Lepus insularis*

The black jackrabbit is found only on Espiritu Santo Island in the Gulf of California, where its status is very little known. Although this is a species with a very restricted distribution, it is unlikely that the island will ever be settled by people and the species is probably less threatened than several other Mexican lagomorphs.

The following priority activities have been identified to ensure the survival of this species:

1. **Status Surveys.** A survey to determine the status of the species is of high priority. This should focus on distribution, population, habitat requirements and probable impacts on the species resulting from introduced animals.
2. **Habitat Management.** An integrated conservation program (emphasizing habitat management) for Espiritu Santo Island should be developed, drawing in part on the results of the survey referred to above.
3. **Research.** Genetic and morphological studies are required to determine the relationship of this species to the black-tailed jackrabbit *L. californicus* from mainland Baja California. Other studies focusing on its basic biology will be useful for long-term conservation and management.
4. **Establishment of Second Population.** As a security against unforeseen catastrophe (such as disease), it would be wise to establish a second population on a nearby island, providing that it can be demonstrated that serious ecological risks will not result from such an introduction.

Tres Marias Rabbit *Sylvilagus graysoni*

This species is endemic to the Tres Marias Islands, approximately 86km from mainland Nayarit. Two subspecies have been recognized: *S. g. graysoni* found on the islands of Maria Madre, Maria Magdalena and Maria Cleofas; and *S. g. badistes* found only in San Juanito island.

The following priority activities have been identified to ensure the survival of this species:

1. **Habitat Conservation and Management.** The main threats to the Tres Marias rabbit are habitat alterations (principally forest clearance) caused by introduced species and human settlements (including the high security prison), and hunting. Large areas of natural vegetation have already been removed on Maria Madre and Maria Cleofas. Extensive habitat perturbations associated with the plans to convert large pristine areas into new human

settlements and agriculture will undoubtedly have a profound impact on the populations of this species. The key factor in ensuring the long term conservation of the Tres Marias rabbit is the protection of its habitat. Reserves of sufficient size for viable populations of this species should be established on Maria Madre. The uninhabited 'Maria Cleofas and San Juanito islands should be managed in their entirety as nature reserves. This would entail a cancellation of plans to settle Maria Cleofas. These recommended new reserves would also protect other endemic species such as the Tres Marias raccoon *Procyon insularis* and the rice rat *Oryzomys nelsoni*. The new Ecological Reserve recently designated by the Mexican government on Maria Magdalena should be assessed for its value in conserving the Tres Marias rabbit.

2. **Status Surveys.** There are no quantitative data on the present status of this species on any of the four islands. Rabbit populations are, apparently, larger on the two islands without human settlements. A survey to determine its present status, population densities and precise habitat requirements is urgently needed.
3. **Research.** The only research so far carried out on this species concerns its taxonomy. Studies of its basic biology and life history, and long term monitoring of its population dynamics are recommended. Particularly important is the study of the ecological interactions between introduced species (e.g., goats, rats) and the Tres Marias rabbit, and the response of this species to habitat disturbance caused by humans. There is also a need to ascertain the extent of reserves required to protect genetically and demographically viable populations.

Omiltemi Rabbit *Sylvilagus insonus*

The Omiltemi rabbit may be among the most endangered rabbits in the world; fewer than ten specimens, all collected during the last century, are known to science. It is known only in the Sierra Madre del Sur, in the vicinity of Omiltemi, Guerrero, Mexico, at elevations between 2,300m and 5,280m.

The following priority activities have been identified for the conservation of this species:

1. **Status Surveys.** Intensive surveys are needed to ascertain whether or not this species survives and to determine its present distribution. These surveys should also focus on habitat requirements and make an assessment of the threats to its survival. Until such information becomes available, a comprehensive conservation strategy cannot be developed.
2. **Habitat Conservation and Management.** The species is restricted to pine and pine-oak forests. Although Omiltemi has been recently declared a State Reserve by the

Mexican government, habitat destruction is probably still a major threat to native species since the coniferous forests have been highly modified and fragmented by intense forestry and cattle grazing.

3. **Regulation of Hunting.** Hunting is probably a major threat to the Omiltemi rabbit. Biological surveys in the area have shown intensive hunting pressures on rabbits and other species of mammals, though so far there has been a complete lack of information about this species.
4. **Research.** There are no data on the biology of this rabbit. If a population is found, it will be extremely important to study urgently its basic biology and determine the factors that cause its rarity. Data on population dynamics, life history and feeding habits will be very useful for establishing a management plan to ensure its long term preservation.
5. **Captive breeding.** A captive breeding program would be advisable.

San Jose Brush Rabbit *Sylvilagus mansuetus*

The San Jose brush rabbit is restricted to San Jose Island in the Gulf of California, Baja California, Mexico, where its status is unknown.

The following priority activities have been identified for the conservation of this species:

1. **Status Survey.** A survey to assess the status, population and precise habitat requirements of this species is a high priority. Several species of mammals on the islands off Baja California have been depleted as a result of the effects of the introduction of exotic mammals, including competitors and predators. Rats and cats, accidentally introduced to San Jose Island, may pose a serious threat to the survival of this species and this should be investigated. Monitoring population levels at least annually will be useful to check the status of the species.
2. **Eradication of Introduced Species.** A priority action for the preservation of this species is the eradication of the introduced animals from San Jose Island, especially those which are demonstrated to be detrimental to the survival of the San Jose brush rabbit.
3. **Research.** As with several other species of Mexican lagomorphs, the biology of the San Jose brush rabbit is little known. Genetic and taxonomic studies are needed to clarify the relationship between this rabbit and the brush rabbit *S. bachmani* from mainland Baja California. Research is needed to document the natural history, population dynamics and life history of this species, as basis for developing an adequate conservation strategy.

4. **Development of Conservation Program.** Based on the results of the surveys and research outlined above, an integrated conservation program should be developed, including careful habitat management and possibly protected area establishment.

Volcano Rabbit *Romerolagus diazi*

The volcano rabbit, a Mexican endemic, is endangered. Its whole geographic range is restricted to a few mountains west and south of Mexico City. Habitat destruction, fires, hunting and pollution pose a serious threat to its survival. The species has disappeared from many localities, including the Nevado de Toluca volcano. Presently the three areas that support the most important populations are the Iztaccihualtl, Popocatepetl and Pelado volcanoes.

The following priority activities have been identified to ensure the survival of this species:

1. **General Habitat Conservation and Management.** Volcano rabbits require grasslands above the tree level and conifer forests with a dense cover of zacatones (bunch grasses) for food and cover. The survival of the species clearly revolves around the control of burning and overgrazing in the prime "zacaton" habitats and the enforcement of laws that prohibit the catching, sale and hunting of the animal. Forest areas where the volcano rabbit is found are significant not only for this species but also as a reservoir for other endemics. It is also an important zone for life-support systems in the Mexico City region. These forests are crucial as water catchment zones and could be exploited sustainably for timber and other renewable resources. Consideration of these broader issues would promote the protection of volcano rabbit habitats. Habitat restoration may be possible in certain areas and this needs further investigation.



Habitat of the volcano rabbit *Romerolagus diazi* in the grasslands at Volcán, Popocatepetl, Mexico (Photo G. Ceballos)

2. **Protected Area Management.** Volcano rabbit habitats are disappearing so fast that it is extremely important to select a number of areas as new reserves, in addition to those already established. Where possible, these reserves should be connected with corridors of suitable habitat and located across the species' geographic range to ensure the preservation of the highest possible genetic diversity. Within the protected areas and other zones scheduled for future protection, appropriate management needs to start as a matter of high priority. The supervision so far given by the Secretaria de Desarrollo Urbano y Ecología (SEDUE) or the Comisión Coordinadora de Desarrollo Ecológico y Rural in Mexico City (COCODER) to volcano rabbit areas is not sufficient. Provision of necessary staff to manage the Izta-Popo National Park and the Special Protected Zones to the south of Mexico City (Volcan el Pelado and Volcan Tlaloc) is required. Although actions to reduce hunting need to be enforced, ways must be identified of making sustainable exploitation of natural resources compatible with wildlife protection. Controlled burning can be made compatible with the recovery of habitats and the conservation of wildlife.
3. **Education Programs.** Education campaigns at village, national and international levels need to be started. Most local inhabitants are unaware of the protected status of the species. Public awareness of the species' habitat is essential. Information on the impact of land use methods that are incompatible with sustainable development and conservation should be made available to villages adjacent to the core habitats. In particular, villagers need to be provided alternatives to land-use practices that are jeopardizing their own livelihoods. Agricultural extension work is required to demonstrate sustainable and ecologically-sensitive farming practices.
4. **Captive Breeding.** A captive-breeding program in the Chapultepec Zoo, Mexico City, has been very successful, indicating the potential for restoring some of the extirpated populations. More scientific supervision of the captive breeding program is probably required and the number of animals in captivity needs to be built up. The captive breeding program requires close international cooperation between all the institutions concerned and the number of breeding facilities involved should be enlarged. In addition, the value of the captive colonies (particularly at the Mexico City and Jersey Zoos) in creating and fostering public awareness should be further developed. Under no circumstances should the species be introduced as a laboratory animal as suggested by some authors (e.g. Granados, 1981), since this could create a demand that could eventually imperil the wild populations.
5. **Status Survey.** Although the general distribution of the species is well known, intensive and extensive surveys are needed to identify the precise distribution of its popula-

tions, especially in areas where the habitat has been fragmented. These data should be collected with a specific view to planning the necessary network of protected areas and corridors (as outlined above) for this species and other forms of endemic wildlife.

6. **Research.** Studies on population densities of the volcano rabbit throughout its geographic range, habitat relationships, population dynamics and life history are needed to ensure that appropriate management is implemented. There is almost no information on the effect of habitat fragmentation on the genetics and population dynamics of the species. It is particularly important that the interactions between cattle grazing and habitat quality for the volcano rabbit are assessed.

Nepal

Two globally threatened lagomorph species occur in Nepal.

Nubra Pika *Ochotona nubrica*

This enigmatic species occurs in alpine steppe habitats in the Himalayas, as well as in neighbouring China and India. It is very little known.

The following priority activities have been identified for the conservation of this species:

1. **Status Surveys.** A survey should be carried out to assess the status and conservation requirements of this species in the Himalayas, with a view to making conservation recommendations. The ecological requirements of the species are not understood at all.
2. **Conservation Action.** Based on the results of surveys outlined above, appropriate conservation measures should be introduced in the Himalayas.

Hispid Hare *Caprolagus hispidus*

This species is seriously endangered, surviving in a few isolated pockets across the former range of its tall grassland habitat in northern India and southern Nepal. It is threatened by habitat destruction for agriculture, forestry, human settlement, flood control and irrigation schemes, together with the adverse effects of dry season burning, overgrazing and harvesting of remaining tall grasslands.

The following priority activities have been identified to ensure the survival of this species:

1. **Maintenance of Protected Areas.** The continued survival of this species in Nepal depends upon the maintenance of the tall grass habitat in the following protected areas (note

that the species also occurs in India: see that account): Royal Chitawan National Park, Royal Bardia Wildlife Reserve and Royal Suklaphanta Wildlife Reserve. In some other reserves there is heavy overgrazing by cattle, notably the Royal Suklaphanta Wildlife Reserve, and this needs to be brought under control.

2. **Improvement of Habitat Management.** The immediate threats to the relict populations of the hispid hare should be alleviated by a change in reserve management practices, from uncontrolled dry season burning of its tall grassland habitat, to a system of carefully controlled rotational burning such that large areas of suitable habitat (i.e. providing optimal cover, food resources, etc.) are available throughout the year. The detailed formulation of appropriate long-term management plans for these remnant areas of tall grassland should draw on the results of the research programs recommended below.
3. **Status Surveys.** Status surveys are needed for this species in a number of areas that have not previously been investigated. These include several areas of southeastern Nepal, where it is not clear whether the species survives.
4. **Research.**
 - 1: Long-term research programs examining the effects of each of the several disturbance factors (e.g. burning, thatch harvesting and grazing) operating on hispid hare habitat are required to formulate appropriate long-term management plans for the remnants of tall grassland habitat. Research into burning, for example, should investigate the effects of factors such as timing, frequency and soil water content on both the vegetation and the hare populations so that optimum management plans can be developed for individual areas.
 - 2: Long-term studies of the behavioral ecology and reproductive biology of the hispid hare are urgently required, concentrating on habitat requirements, breeding biology and home range use throughout the year (so far only studied in the early dry season). It is important that these studies include the monsoon period when the marshy areas used as refugia during the early dry season post-burn period are likely to be among the first areas to become inundated.
5. **Captive Breeding.** A captive breeding programme for this species needs to be initiated to provide a nucleus of animals for reintroduction into the wild, should this become necessary.

South Africa

Although seven species of Lagomorph occur in South Africa, only the riverine rabbit is of serious conservation concern.

Riverine Rabbit *Bunolagus monticularis*

The riverine rabbit is the only species of lagomorph on the African continent regarded as endangered. This is mainly due to its extremely small numbers and narrow habitat specificity, although habitat clearance appears now to have stopped.

The following priority activities have been identified to ensure the survival of this species:

1. **Habitat Conservation and Management.** The riverine rabbit inhabits dense riparian growth along the seasonal rivers in the central Karoo. Almost 68% of the remaining riverine rabbit habitat is associated with an interconnected network of rivers, principally the Sak, Klein Sak and Riet, Klein Riet in the central Karoo. No national reserve has yet been proclaimed for the species, but recent additions to the Karoo National Park (32°12'S, 22°16'E) may prove suitable for relocation of the species once the vegetation has recovered from the effects of overgrazing. Also, plans to have the farm which has formed the focus of research on the species proclaimed a conservancy under South Africa's Natural Heritage Programme should be implemented. The site (31°21'S, 22°38'E) is situated along the Klein Brak River near the town of Victoria West.
2. **Status Surveys.** No active monitoring of the riverine rabbit population is currently in progress. It is important that a long-term program be established, since although habitat destruction is no longer taking place, the threat of local extinctions of tiny, fragmented populations remains very real.
3. **Education Program.** The riverine rabbit awareness programme that has been initiated amongst the farmers of the central Karoo needs to be continued and expanded.
4. **Research.** A study is needed of the habitat area requirements of the species, focusing in particular on the degree of population fragmentation and the amount of gene flow between nearby populations. Research should also examine the feasibility of rehabilitating habitat in parts of the species' former range, with a view to building up the wild population to a safer level.
5. **Captive Breeding.** The development of a captive breeding program, which will allow the eventual reintroduction of the species into areas of suitable habitat in which it no longer survives or where it has become very rare, is a very high priority. Following recent investigations, it is clear that the captive breeding program should have the following characteristics: (a) an initial founder population of not less than 16 individuals (eight pairs); (b) breeding pairs remain mated for several litters; (c) the offspring from each breeding pair are subsequently systematically mated to members of other litters; and (d) inbreeding and the degree of relatedness is reduced through the periodic

introduction of wild caught individuals into the captive population.

United States of America

One lagomorph of international conservation concern occurs in the United States.

Pygmy Rabbit *Brachylagus idahoensis*

The pygmy rabbit is found through much of the sagebrush habitat of the Great Basin and surrounding areas, where its status varies locally from being highly threatened to common.

The following priority activities have been identified to ensure the survival of this species:

1. **Habitat Conservation and Management.** The main threat to the pygmy rabbit is habitat loss. The removal of big sagebrush to increase forage production or create cropland has greatly reduced and fragmented the available habitat. Pygmy rabbits require dense sagebrush, for both food and cover, and soft soils for burrowing. Where population levels have become small and fragmented, nature reserves should be established and, where possible, connected by corridors of sagebrush cover. Fire can destroy the habitat and a fire protection plan should be developed for each critical site. In general, cattle-grazing is incompatible with the conservation of pygmy rabbit habitat, except in areas that have become so open that grazing is likely to increase the sagebrush density. The conservation of this species will therefore require compromises with livestock interests; these might include protecting the densest deep soil sagebrush areas and a surrounding buffer zone (of several hectares), which should be sufficient to maintain viable populations. Management plans should aim to ensure that such protected sites are not too widely scattered, thereby permitting some genetic interchange between subpopulations.
2. **Habitat Restoration.** Where sagebrush habitat has been removed, efforts should be made to restore it. In some regions, such as Douglas County, Washington, this may occur through natural succession; in other regions planting may be needed. In either case, twenty or more years may be required for this program. Restoration should be carried out adjacent to sites occupied by the species to increase the size of the conservation area and to reduce the fragmentation of populations.
3. **Research.** Most past research has been directed at understanding the natural history and behavior of the pygmy rabbit. This has contributed important information for management, such as the importance of big sagebrush. The highest research priority now is to determine the dispersal capability of the pygmy rabbit and how different

levels of habitat fragmentation relate to the genetic isolation of subpopulations. This should enable managers to plan for the correct areas and configurations of habitat patches needed to support genetically and demographically viable populations.

4. **Status Surveys.** The status of the pygmy rabbit varies widely across its range. In southern Idaho, it is considered secure and locally common. By contrast, in Washington it occurs only at three known sites in one county and is considered threatened. Throughout the rest of its range its status probably lies between these extremes, but in general its distribution is reduced from historic levels. Survey efforts are needed, especially in areas where habitat has been fragmented, to determine the pygmy rabbit's status more accurately.

Conservation of Other Species of Concern

In addition to the globally threatened species listed above, there are another 21 species of conservation concern. These are discussed below on a country-by-country basis. In most cases, they are too poorly known to assess conservation needs without additional survey work, though it is believed that they are less seriously threatened than the species listed in the previous section.

Afghanistan

Turkestan Red Pika *Ochotona rutila*. This species occurs in low numbers in fragmented populations in the Soviet Union. Its status and conservation requirements in the mountains of Afghanistan are poorly known and need to be assessed.

Bhutan

Forrest's Pika *Ochotona forresti*. This is a very little known species occurring in forested regions at high altitude, as well as in Burma, China and India. Its conservation status needs to be assessed; it is possibly a subspecies of Royle's pika *O. roylei*.

Burma

Forrest's Pika *Ochotona forresti*. This is a very little known species occurring in forested regions at high altitude in the north of the country, as well as in Bhutan, China and India. Its status needs to be assessed.

China

Alpine Pika *Ochotona alpina*. Although this species as a whole is not of conservation concern, three of its subspecies are. *O. a. argentata* is known only from the Helan Shan area near the borders of the Ningxia, Hexizoulang and Gansu

Provinces, where it might be at risk from vertebrate control programs and habitat clearance, in addition to having a tiny, isolated and possibly inviable population (there have been no records for over 50 years). No information is available on *O. a. nitida* (see account under Soviet Union) and there is an undescribed subspecies (see account under Mongolia).

Gansu Pika *Ochotona cansus*. Although this species as a whole is not of conservation concern, two of its subspecies are. *O. c. sorella* is restricted to the Yunzhong Shan in Shaanxi Province, where it is probably threatened by habitat loss and vertebrate extermination programs, in addition to having a tiny, isolated and possibly inviable population (there have been no records for over 50 years). *O. c. morosa* is restricted to the Tsing Ling Shan in Shaanxi Province, where the population is probably small, isolated and vulnerable, though there is no recent information on its status.

Forrest's Pika *Ochotona forresti*. This is a very little known species occurring in forested regions at high altitude in northwest Yunnan and Southeast Xizang Provinces, as well as in neighbouring Bhutan, Burma and India. Its status needs to be assessed.

Glover's Pika *Ochotona gloveri*. This species occurs in talus habitat at high altitudes in southwest Qinghai, northeast Xizang, northwest Yunnan and western Sichuan Provinces. Nothing is known of its conservation requirements, and research could show that it is closely related to the red-eared pika *O. erythrotis*.

Himalayan Pika *Ochotona himalayana*. This pika is known only from the Mount Jolmolungma (Mount Everest) area in southern Xizang. It is possibly a subspecies of Royle's pika *O. roylei*. Its conservation requirements are unknown.

Ladak Pika *Ochotona ladacensis*. This species is restricted to barren areas at very high elevations in Qinghai, Xizang and Xinjiang Provinces, as well as in neighbouring India. It is not known whether it faces any conservation problems.

Pallas's Pika *Ochotona pallasii*. Although this species as a whole is not of conservation concern, three of its subspecies are. *O. p. hamica* occurs on isolated mountains in the Gobi Desert in China (Xinjiang Province) and Mongolia, and is probably threatened by climate change, habitat degradation and population fragmentation. *O. p. pricei* is heavily controlled through vertebrate extermination near the Mongolian border (also occurs in Mongolia and the Soviet Union). *O. p. sunidica* is extremely isolated and is likely to be at risk from vertebrate extermination programs and habitat alteration.

Steppe Pika *Ochotona pusilla*. Though not definitely known to occur in China, it might do so on the southern slopes of the Tarbagatai Mountains, and this requires investigation. For further details of the species, see under Soviet Union.

Turkestan Red Pika *Ochotona rutila*. This species occurs in low numbers in the Soviet Union. Whether it occurs in the mountains of Xinjiang Province needs to be determined, along with its conservation requirements.

Moupin Pika *Ochotona thibetana*. Although this species as a whole is not of conservation concern, two of its subspecies are. *O. t. huangensis* is restricted to the Tsing Ling Shan in Shaanxi Province, where the population is probably small, isolated and vulnerable, though there is no recent information on its status. For details of *O. t. sikimaria*, see account under India.

Hainan Hare *Lepus hainanus*. This species is restricted to Hainan Island, where its populations have been reduced through overhunting and agricultural expansion. A survey of its status is needed, and public education programs might be necessary to supplement protection measures. The relationships of this hare to other Asian species need to be assessed.

Manchurian Hare *Lepus mandshuricus*. Though widely distributed in China (Manchuria) and adjacent parts of the Soviet Union, the forest habitat of this hare is being cleared rapidly. It is important to assess the effectiveness of existing reserves for safeguarding this species.

Manchurian Black Hare *Lepus melainus*. This hare is restricted to a smaller area within the range of the previous species and the taxonomic relationships between the two need to be clarified. Its conservation requirements are unknown.

Costa Rica

Dice's Cottontail *Sylvilagus diceri*. This species is restricted to high elevations in Costa Rica and Panama. Nothing is known of its status or conservation requirements and these should be assessed.

Ethiopia

Ethiopian Hare *Lepus fagani*. This species occurs at high altitudes in northern and western Ethiopia, and also in Kenya; it is probably not threatened, but in view of its relatively restricted range, its status should be periodically monitored. Its relationship to other African hare species should be studied, since it might not be a valid species.

Ethiopian Highland Hare *Lepus starcki*. This species is restricted to high altitudes in the central Ethiopian highlands, where it is probably not threatened. However, it needs to be monitored in view of its small range. Its relationship to other African hare species also needs to be studied.

India

Forrest's Pika *Ochotona forresti*. This is a very little known species occurring in forested regions at high altitude in Assam and Sikkim, as well as in neighbouring Bhutan, Burma and China. Its status needs to be assessed.

Ladak Pika *Ochotona ladacensis*. This species is restricted to barren areas at very high elevations in Kashmir, as well as in neighbouring China. It is not known whether it faces any conservation problems.

Moupin Pika *Ochotona thibetana*. Although this species as a whole is not of conservation concern, two of its subspecies are. *O. t. sikimaria* is known only from Sikkim where its rhododendron thicket habitat has been severely damaged, perhaps bringing this race to the verge of extinction. For details of *O. t. huangensis* see account under China.

Indonesia

Indian hare *Lepus nigricollis*. In Java hares are restricted to the extreme west of the island and are declining. Because they were thought to have been introduced from India, they have been of no conservation concern. The recent suggestion from fossil evidence that they may be endemic changes this view. Taxonomic and historical research is urgently needed to clarify their status before they become extinct.

Kenya

Ethiopian Hare *Lepus fagani*. This species occurs at high altitudes mainly in northern and western Ethiopia and also in northern Kenya; it is probably not threatened, but in view of its relatively restricted range, its status should be periodically monitored. Its relationship to other African hare species should be studied, since it might not be a valid species.

Mexico

White-sided Jackrabbit *Lepus callotis*. This species is largely confined to Mexico, where it has a wide distribution, but it could be at risk due to changes in its open grassland habitat. Small, declining populations survive in New Mexico, United States. Overgrazing by livestock tends to result in an increase in shrubs, thus favoring the black-tailed jackrabbit *L. californicus* instead.

Mongolia

Alpine Pika *Ochotona alpina*. Although this species as a whole is not of conservation concern, three of its subspecies are. For details of *O. a. argentata* and *O. a. nitida* see accounts

under China and the Soviet Union). There is an undescribed subspecies which is known only from the Bajan Ulan Mountains, where its status is unknown and needs to be assessed.

Pallas's Pika *Ochotona pallasii*. Although this species as a whole is not of conservation concern, three of its subspecies are. *O. p. hamica* occurs on isolated mountains in the Gobi Desert in Mongolia and China (Xinjiang Province) and is probably threatened by climate change, habitat degradation and population fragmentation. *O. p. pricei* occurs in the Choyr Mountains, where populations are now very depressed and threatened (though numbers may be higher in China and the Soviet Union). For *O. p. sunidica* see account under China.

Pakistan

Ladak Pika *Ochotona ladacensis*. This species is restricted to barren areas at very high elevations in neighbouring China and India. It is not known whether it occurs as far west as Pakistan, nor whether it faces any conservation problems.

Panama

Dice's Cottontail *Sylvilagus dicei*. This species is restricted to high elevations in western Panama and Costa Rica. Nothing is known of its status or conservation requirements and these should be assessed.

Soviet Union

Alpine Pika *Ochotona alpina*. Although this species as a whole is not of conservation concern, three of its subspecies are: *O. a. argentata* (see account under China); *O. a. nitida*, which has an isolated and restricted distribution which may place it at risk, and so its status should be evaluated; and an undescribed subspecies (see account under Mongolia).

Steppe Pika *Ochotona pusilla*. This species is not globally threatened, but its range has declined considerably in historical times, possibly as a result of the modification of its preferred steppe-shrub habitat. However, research is needed to investigate the reasons for its decline more thoroughly and to assess the actions required to secure its populations in the future.

Pallas's Pika *Ochotona pallasii*. Although this species as a whole is not of conservation concern, three of its subspecies are. For details on *O. p. hamica* see accounts under China and Mongolia. *O. p. pricei* was formerly heavily controlled in southwestern Tuva ASSR (also occurs in China and Mongolia). For *O. p. sunidica*, see account under China.

Turkestan Red Pika *Ochotona rutila*. This species occurs in low numbers in fragmented populations in parts of the Uzbek, Tadzhik, Kirgiz and Kazakh SSRs, and perhaps in neighbouring Afghanistan and China. Its conservation requirements are poorly known and need to be assessed.

Manchurian Hare *Lepus mandshuricus*. Though widely distributed in China (Manchuria) and adjacent parts of the Soviet Union, the forest habitat of this hare is being cleared rapidly. It is important to assess the effectiveness of existing reserves for safeguarding this species.

Manchurian Black Hare *Lepus melainus*. This hare is restricted to a smaller area within the range of the previous species and the taxonomic relationships between the two need to be clarified. Its conservation requirements are unknown.

Spain

Broom Hare *Lepus castroviejoi*. This poorly differentiated species is restricted to the Cantabrian Mountains in northern Spain. It is probably not threatened at present, though hunting in the west of its range should be restricted. Its relationships with the European hare require closer investigation.

United States

American Pika *Ochotonaprinceps*. Although this species as a whole is not of conservation concern, four of its subspecies are: *O. p. goldmani*, *O. p. nevadensis*, *O. p. obscura* and *O. p. tutelata*. These have isolated populations which may be at risk. The population from the type-locality for *O. p. tutelata* has disappeared and recent studies have shown that *O. p. nevadensis* may have lost most, or all, of its genetic variability.

White-sided Jackrabbit *Lepus callotis*. This species is largely confined to Mexico, where it has a wide distribution but could be at risk due to changes in its open grassland habitat. Small, declining populations survive in New Mexico. Overgrazing by livestock tends to result in an increase in shrubs, thus favoring the black-tailed jackrabbit *L. californicus* instead.

Alaskan Hare *Lepus othus*. This species appears to have declined in numbers and work is needed to assess its status and conservation requirements. It is probably conspecific with the Arctic hare *L. arcticus*, and this needs to be clarified.

New England Cottontail *Sylvilagus transitionalis*. This species occurs in the higher parts of the Appalachian chain and its status varies considerably locally. The genetics and taxonomic status of this species need clarification, as well as its supposed competitive relationship with the eastern cottontail *S. floridanus*. Detailed investigations into the habitat requirements of the New England cottontail are needed in order to develop management programs.

Marsh Rabbit *Sylvilagus palustris*. This species is common throughout most of its range. However, the Lower Keys marsh rabbit, *S. p. hefneri* is an endangered subspecies. The taxonomic status of this insular form as well as its biology, ecology and habitat requirements need thorough study.

Priorities for Conservation-Related Research on Lagomorphs

In addition to all the activities listed above, some general research approaches are needed to underpin conservation efforts on behalf of the lagomorphs. These are as follows:

Taxonomy

The systematics of the two genera, *Ochotona* (the pikas) and *Lepus* (the hares and jackrabbits) is highly confused, making it difficult to assess conservation priorities between species. This is also true, to a lesser extent, with *Sylvilagus* (the cottontails). A cladistic analysis, using mitochondrial DNA, should be performed as a means of resolving these problems. This analysis would entail the collection of tissues from all species and subspecies; analyses could be performed at the Smithsonian Institution or a number of other laboratories in the United States, or elsewhere.

Survey

Field surveys should be carried out to assess the status and conservation requirements of all the globally threatened lagomorph species and all other species of conservation concern listed above. The aim of these surveys should be to ensure that all conservation actions are based on the best possible data, including biological, ecological, sociological, economic and political aspects.

Biology of Small Populations

To assess the nature of insularisation of pika populations, a joint research program should be initiated between United States, Soviet, Chinese and/or Mongolian biologists. This research program would address the effect of "island" size and degree of isolation in terms of population viability analysis

(including a genetic analysis of each population). These data will form a benchmark against which extinction probabilities of isolated populations of pikas can be assessed. The data should also be robust and useful for the assessment of other similarly isolated taxa. This work should start with the pikas but should be expanded to include other lagomorph species and populations as appropriate.

Assessment of Pika Control Programs

There is an urgent need to carry out a full environmental impact assessment of the mammal control programs being carried out in central Asia. This assessment should consider the costs and benefits of these programs from the following aspects: risks to threatened species (including pikas); risks to economically valuable species; effects on rangeland management; effects on human health; and impact on the livestock industry and on agriculture. The assessment should produce guidelines for the best management options for the areas in which the control programs are taking place, from both the human welfare and biological conservation viewpoints.

Setting Offtake Quotas for Commercially Valuable Lagomorphs

Certain lagomorph populations appear to be harvested at rates too high to be sustained. In these cases it is necessary to establish long-term monitoring programs and set annual quotas based on the best possible scientific data. This program is a particularly high priority for European hare populations in most European countries.

Reconciling Agricultural Practices with Lagomorph Management

Research is needed to determine how agricultural improvements can be made in ways that do not jeopardize lagomorph populations, including game species. Again, this is a high priority for the brown hare in Europe.

Appendix 1

IUCN/SSC Lagomorph Specialist Group Statement on the Introduction of Exotic Lagomorphs

The Lagomorph Specialist Group strongly opposes the deliberate or accidental release into the wild of exotic lagomorphs. There can be no argument in support of the translocation of foreign species from continent to continent for hunting or fur farming without thorough examination of all aspects of any such plan, including security en-route and after liberation and environmental side-effects on other biota. Even translocations for conserving rare species must be subject to strict health and environmental controls.

IUCN/SSC Lagomorph Specialist Group Statement on the Use of Biological Control of Lagomorphs

The Lagomorph Specialist Group of the IUCN strongly opposes the deliberate use of any disease, parasite, or predator to control lagomorph populations in the absence of a detailed understanding of the aetiology, epidemiology, specificity and humaneness of the control agent. Field work as well as laboratory trials are necessary to investigate all possible side-effects. The Group believes that only in the light of this information could soundly based judgments be made on whether to use any biological control agent.

IUCN/SSC Action Plans for the Conservation of Biological Diversity

1. Action Plan for African Primate Conservation: 1986-1990. Compiled by J.F. Oates and the IUCN/SSC Primate Specialist Group, 1986, 41 pp., £ 7.50, U.S.\$ 15.00. Out of print.
2. Action Plan for Asian Primate Conservation: 1987-1991. Compiled by A.A. Eudey and the IUCN/SSC Primate Specialist Group, 1987, 65 pp., £ 7.50, U.S.\$ 15.00.
3. Antelopes. Global Survey and Regional Action Plans. Part 1. East and Northeast Africa. Compiled by R. East and the IUCN/SSC Antelope Specialist Group, 1988, 96 pp., £ 7.50, U.S.\$ 15.00.
4. Dolphins, Porpoises and Whales. An Action Plan for the Conservation of Biological Diversity: 1988-1992. Second Edition. Compiled by W.F. Perrin and the IUCN/SSC Cetacean Specialist Group, 1989, 27 pp., £ 5.00, U.S.\$ 10.00.
5. The Kouprey. An Action Plan for its Conservation. Compiled by J.R. MacKinnon, S.N. Stuart and the IUCN/SSC Asian Wild Cattle Specialist Group, 1988, 19 pp., £ 5.00, U.S.\$ 10.00.
6. Weasels, Civets, Mongooses and their Relatives. An Action Plan for the Conservation of Mustelids and Viverrids. Compiled by A. Schreiber, R. Wirth, M. Riffel, H. van Rompaey and the IUCN/SSC Mustelid and Viverrid Specialist Group, 1989, 99 pp., £ 7.50, U.S.\$ 15.00.
7. Antelopes. Global Survey and Regional Action Plans. Part 2. Southern and South-central Africa. Compiled by R. East and the IUCN/SSC Antelope Specialist Group, 1989, 96 pp., £ 7.50, U.S.\$ 15.00.
8. Asian Rhinos. An Action Plan for their Conservation. Compiled by Mohd Khan bin Momin Khan and the IUCN/SSC Asian Rhino Specialist Group, 1989, 23 pp., £ 5.00, U.S.\$ 10.00.
9. Tortoises and Freshwater Turtles. An Action Plan for their Conservation. Compiled by the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group, 1989, 47 pp., £ 7.50, U.S.\$ 15.00.
10. African Elephants and Rhinos. Status Survey and Conservation Action Plan. Compiled by D.H.M. Cumming, R.F. du Toit, S.N. Stuart and the IUCN/SSC African Elephant and Rhino Specialist Group, 1990, 73 pp., £ 7.50, U.S.\$ 15.00.
11. Foxes, Wolves, Jackals, and Dogs. An Action Plan for the Conservation of Canids. Compiled by J.R. Ginsberg, D.W. Macdonald, and the IUCN/SSC Canid and Wolf Specialist Groups, 1990, 116 pp., £ 7.50, U.S.\$ 15.00.
12. The Asian Elephant. An Action Plan for its Conservation. Compiled by C. Santiapillai, P. Jackson, and the IUCN/SSC Asian Elephant Specialist Group, 1990, 79 pp., £ 7.50, U.S.\$ 15.00.
13. Otters. An Action Plan for their Conservation. Compiled by P. Foster-Turley, S. Macdonald, C. Mason and the IUCN/SSC Otter Specialist Group, 1990, 124 pp., £ 7.50, U.S.\$ 15.00.
14. Antelopes. Global Survey and Regional Action Plans. Part 3. West and Central Africa. Compiled by R. East and the IUCN/SSC Antelope Specialist Group, 1990, 169 pp., £ 7.50, U.S.\$ 15.00.

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