The World of Pikas

ANDREW T. SMITH

Introduction

The 30 currently recognized living species of pika (Ochotonidae: Genus *Ochotona*) comprise approximately one-third of all lagomorphs. The Leporidae, in contrast, contains 32 species of hare (Genus *Lepus*) and 29 species of rabbit (multiple genera; Hoffmann and Smith 2005). Both traditional (morphological) and molecular evidence indicates that the Ochotonidae separated from the Leporidae during the Oligocene, approximately 37 Mya. The Ochotonidae originated in Asia, but had spread to North America by the late Oligocene. Throughout their Holarctic range, and even extending into northern Africa, pikas differentiated and became quite diverse during the Miocene. Modern pikas (*Ochotona*) first appeared in Asia during the early Pliocene and spread to North America by the mid-Pliocene. The only two pika genera to appear in historical times, *Prolagus* and *Ochotona*, appeared in Europe by the late Pliocene. Following the extinction of *Prolagus*, *Ochotona* became the only living representative of the family that had flourished with as many as 25 fossil genera (Dawson 1967; Erbajeva 1988, 1994).

Today's pikas are found primarily in the high mountains of western North America (two species) and across Asia (28 species; Smith et al. 1990; Hoffmann and Smith 2005). The "hotspot" for *Ochotona* is China, home to 24 species. No consensus has been reached on the systematics of *Ochotona*; in fact, no two revisions of all or part of the genus are remotely similar (Smith et al. 1990; Yu et al. 2000). Molecular approaches are beginning to unravel the Gordian knot of pika systematics, but much remains to be clarified (Yu et al. 2000; Niu et al. 2001, 2004). We do know that most pikas are remarkably similar in morphology and that they generally live in some of the most remote landscapes on earth.

The purpose of this review is to bring attention to pika biology by demonstrating some of the important issues in ecology, behavior, and conservation that can be addressed by studying pikas. It is distressing that only three of the 174 presentations at the Second World Lagomorph Conference held in Portugal (1.7%) were focused on pikas, whereas 33% of papers should have been on pikas if they had been represented according to their species richness within

School of Life Sciences, Box 874501, Arizona State University, Tempe, AZ, USA; E-mail: a.smith@asu.edu

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the Lagomorpha (Alves and Ferrand 2004). In addition, most practitioners of the leporids fail to compare their results with the ochotonids. Similarly, while pikas are clearly “small mammals,” those studying the more abundant rodents also generally do not compare their findings with those of pikas. The comparative method is a powerful tool in biology, and the failure to utilize pikas as a robust and independent lineage for comparisons is regrettable. This review will show that pikas represent an exciting group of animals to study.

What is a Pika?

Pikas are small egg-shaped animals with prominent round ears and no visible tail. Pikas are fairly uniform in size with body mass ranging generally from 70 to 300 g among species. There is little sexual dimorphism. Pikas that have been studied have relatively high body temperatures, and most species appear to be quite sensitive to high ambient temperatures (Smith 1974a; MacArthur and Wang 1973, 1974). Most pikas are diurnally active. Like other lagomorphs, they do not hibernate. Pikas are generalized herbivores and they produce two types of feces like their leporid cousins—dry round hard pellets and a soft dark viscous caecotroph. Most species construct caches of vegetation during the short summer and live off of these stores (called haypiles) during the winter (Millar and Zwickel 1972; Conner 1983; Huntly et al. 1986; Dearing 1997). Another trait characteristic of pikas, but not of most other lagomorphs, is their propensity to vocalize (Conner 1985; Smith et al. 1986). Several morphological characteristics distinguish ochotonids from leporids: (1) small size (head-body length generally <285 mm, whereas leporids are all >300 mm); (2) the short round ears (<40 mm) compared with long ear pinnae (>60 mm) in leporids; (3) concealed tail versus short but evident tail in leporids; (4) skull without supraorbital process versus a skull with supraorbital processes in leporids; and (5) two pairs of upper premolars versus three pairs of upper premolars in leporids.

Pikas occupy two distinctly different habitats: rock piles and talus versus meadow and steppe, and our understanding of pika biology necessarily begins with a comparative examination of the life history characteristics expressed by rock-dwelling and meadow-dwelling pika species.

Rock-Dwelling Versus Meadow-Dwelling Pikas

All North American pikas and about half of the species in Asia live in rocky habitats and forage in adjoining meadows or patches of vegetation interspersed within the rocks; these are generally non-burrowing forms (Formozov 1981; Smith 1988). In contrast, approximately half of the Asian species occupy meadow or steppe habitats where they characteristically make burrows (Smith 1988). These habitat types are blurred in some cases; there are a few forms (such as the Afghan pika, *Ochotona rufescens*, and Pallas's pika, *Ochotona pallasi*) that occupy open habitats where they make burrows, but that can also be found in rocky areas. These "intermediate" species are not characterized by an intermediate suite of life history traits between those of rock and meadow-dwelling pikas; instead, they adopt the life history characteristics of meadow/burrowing pikas (Smith 1988). Some populations of rock-dwelling pikas live in what first seem to be atypical habitats such as piles of logs or moss covered boulders (common in the Northern pika, *Ochotona hyperborea*), old walls (Glover's pika, *Ochotona gloveri*; Chinese red pika, *Ochotona erythrotis*), or detritus left by human occupation (American pika, *Ochotona princeps*). In these cases, it is apparent that the pikas are keying in on the disruptive nature of the habitat, as their life history traits otherwise match those of pikas living in pure talus environments.

Elsewhere, I have reviewed in detail the species that fall into these two dramatically different eco-types of pika species (Smith 1981a, 1988; Smith et al. 1990). Pika species typically found in rocky habitats are the Alpine pika (*Ochotona alpina*), Collared pika (*Ochotona collaris*), Chinese red pika (*O. erythrotis*), Glover's pika (*O. gloveri*), Himalayan pika (*Ochotona himalayana*), Northern pika (*O. hyperborea*), Ili pika (*Ochotona iliensis*), Large-eared pika (*Ochotona macrotis*), American pika (*O. princeps*), Royle's pika (*Ochotona roylei*), and Turkestan red pika (*Ochotona rutila*). Typical meadow-steppe burrowing pikas include the Gansu pika (*Ochotona cansus*), Plateau pika (*Ochotona curzoniae*), Daurian pika (*Ochotona dauurica*), Kozlov's pika (*Ochotona koslowi*), Ladakh pika (*Ochotona ladacensis*), Muli pika (*Ochotona muliensis*), Nubra pika (*Ochotona nubrica*), Moupin pika (*Ochotona thibetana*), and Thomas' pika (*Ochotona thomasi*). In this review I will concentrate on comparisons between the rock-dwelling American pika and meadow-dwelling Plateau pika, two species on which I have worked extensively, because they present a clear contrast in ecology, reproduction, and behavior. Gliwicz et al. (2005) provide a comparison between the rock-dwelling pikas in North America and Asia.

Ecological Relationships

American pikas occupy individual territories at low density (generally 8–10/ha) on talus habitat (Smith and Ivins 1984; Smith and Weston 1990). There is no significant difference in territory size between males and females, although males are more likely than females to roam across the talus beyond the confines of their territory. Territory size remains remarkably constant across the geographic range of the species. Nearest-neighbor distances between centers of activity on territories range from about 14 to 30 m. Home ranges appear to be about twice the size of territories, although both measurements are sensitive to the method used for their determination (Smith and Ivins 1984; Smith and Weston 1990). There is a general trend for territories to be smaller when vegetation bordering the talus is more productive compared with larger territories in less productive settings (Millar and Zwickel 1972; Millar 1973). Additionally, territories of American pikas are more likely to be found near the talus/vegetation interface than deeper into the talus, where animals would have a longer distance to travel to feed or secure vegetation for their haypiles. One of the primary differences between the rock-dwelling pikas of North America and those from Asia is that Asian forms tend to live as pairs, although even in these situations there are few direct social interactions between the male and female of the pair (Kawamichi 1970; Smith 1981a; Nikolskii and Mukhamediev 1997; Gliwicz et al. 2005).

Plateau pikas, in contrast, live in social family groups on alpine meadows across the Qinghai-Xizang plateau (Smith et al. 1986; Smith and Wang 1991; Dobson et al. 1998, 2000). These family group territories consist of a traditional communal burrow system on which adult males and females live (in various combinations; see below) and their young of the year. Approximately 25 m separates the center of activity of a family group from that of each of the surrounding family groups. Regional density may approximate 300/ha following the reproductive season, although density at this time is highly variable among years. Density is also variable seasonally within single years, as high overwinter mortality knocks the population down to a low level just prior to the onset of reproduction (Wang and Smith 1988). This overwinter mortality is particularly severe in years with unusually deep snow, a situation that leads to strong inter-year differences in density (Wang and Smith 1988).

In summary, American pikas live at low density, but they are long-lived (some individuals live 6 years; Smith 1974b, 1978). These dynamics ensure that population density is relatively constant among years. Most Plateau pikas are short-lived (almost all breeding age animals are 1 year old) and populations fluctuate greatly on a seasonal and annual basis. Their populations may reach extremely high densities.

Reproduction

All aspects of reproductive performance in American pikas converge to yield a very low annual production of offspring (Millar 1973, 1974; Smith 1978). While two litters are initiated each breeding season, only one is successfully weaned. Normally the first litter is successful and the second litter is lost after parturition. Pika mothers put on fat during the gestation of their first litter and these energy resources are utilized during weaning. Thus, second litters, normally conceived following a post-partum estrus, are born when their mother's fat (energy) reserves have been used up. This typically leads to abandonment of the second litter. However, if a mother has lost her first litter to a predator or has abandoned it for other reasons (such as when resources are insufficient; Smith 1978; Smith and Ivins 1983), second litters appear to be a safety valve.

Litters are also small and average three (range 1–5) in American pikas. Due to the energetic constraints of weaning, there can be a gradual decrease of litter size due to pre-implantation losses, resorbtion of embryos, or losses during weaning. The end result is the production of approximately two young per mother per year (Millar 1973, 1974; Smith 1978). In contrast, Plateau pika mothers are baby machines, churning out fairly large litters (generally 4–8 young) at 3-week intervals during the reproductive season. Several litters (normally at least three) are produced each year, and most young are weaned successfully. The result is an increasing density within family burrow territories as the breeding season progresses, thus a high regional population density (Smith and Wang 1991; Dobson et al. 1998).

Social Dynamics

The solitary American pika is notoriously unsocial. I have spent hundreds of hours directly observing populations of American pikas that were all individually marked with colored ear tags. Observed social interactions are normally aggressive, with territory holders (male or female) chasing out intruding conspecifics (Smith 1981b, 1984; Smith and Ivins 1984). There are some "rules" however to these chases. Most pikas reside in territories adjoining an animal of the opposite gender, and chases occur only half of the time when these animals encounter one another. The same is true of their offspring—sometimes they are chased but at other times tolerated. On the other hand, animals that reside more than one territory away are nearly always chased. The talus and the pika territories are of sufficient size, however, that these chases occur on average only once in about 15 h of observation (Smith and Ivins 1984). There are further nuances in the social-spatial dynamics of American pikas; animals are more likely to intrude onto the territories of neighbors if the neighbor is not surface active at that time. This appears to be a tactic to avoid detection and the resultant long chase that may ensue (Smith and Ivins 1986; see Smith and Ivins 1987 for similar spatial temporal relationships between parents and offspring).

While no true social interactions can be observed between conspecific American pikas, there is one telltale behavior that characterizes the social system on a rock slope. About 95% of all instances when two pikas encounter one another and no chase ensues (a behavior category I have termed "social tolerance"), are between nearest neighbors of opposite gender (Smith and Ivins 1984). Similarly, nearly all occurrences of pikas duets are between male and female nearest neighbors (Smith and Ivins 1984). Thus, American pikas can and do discriminate among animals that may be a mating partner from others in the local population.

The social system of the Plateau pika could not be more different than that of the American pika. Plateau pikas are extremely social, and when the population density has peaked (following the weaning of a second or third litter), affiliative social interactions can be observed at the rate of one per minute (Smith et al. 1986; Smith and Wang 1991). These affiliative behaviors include allogrooming, sitting in contact, nose rubbing, and many other forms of contact. In addition, Plateau pikas utter up to six different vocalizations, many of which elicit these affiliative contact behaviors (Smith et al. 1986). Most of the interactions occur among juveniles of the same or different age, and many include an adult male (or putative father) on the family territory. Rate of expression of affiliative behavior by adult males is higher than for adult females. Over 95% of all affiliative behaviors observed in a population occur within family groups (Smith et al. 1986; Smith and Wang 1991; Dobson et al. 1998). In contrast, aggressive behaviors (long chases and fights) are normally expressed by animals from different family territories (normally these are adult male interactions; Smith et al. 1986; Smith and Wang 1991).

Dispersal and Population Structure

Intriguingly, one similarity between American and Plateau pikas (and indeed, all pika species that have been studied to date) is the degree to which individuals are sedentary. Stated another way, pikas are relatively poor dispersers. They are most likely to stay at or near their site of birth (remain philopatric), and dispersing animals normally do not range far from their natal territory. The American pikas I observed in the Rocky Mountains of Colorado rarely dispersed (Smith 1974b; Smith and Ivins 1983; Smith 1987). Over 85% of all adults that controlled access to a territory remained there for life. Of 45 juveniles born into our population over 3 years, only two dispersed (4%) within their home talus. Dispersal between talus patch habitats also appears to be an infrequent phenomenon (Tapper 1973; Smith 1987; Peacock 1997). Because American pikas are individually territorial and long-lived, openings (resulting from death of a territory resident) are rare and apparently normally claimed by animals born nearby who have the greatest familiarity with the socio-spatial structuring on the talus (Smith and Ivins 1983; Peacock and Smith 1997). One interesting consequence of the eventual settlement pattern of pikas into these vacancies is that they are normally claimed by animals of the same sex as the previous occupant and the apparent “locked in” structure of the population is normally an alternate male-female pattern (Smith and Ivins 1983, 1984). The only exception to this structure in the literature comes from a population that was a “dispersal sink” and had high mortality (thus multiple available sites) each year, so that neighboring animals could not control the eventual settlement pattern of dispersers (Brown et al. 1989; Brown, personal comm.).

Plateau pikas are also primarily philopatric (Smith and Wang 1991; Dobson et al. 1998). Few adults move to new family territories between years (because of the high mortality, few are available for such movements). Young remained in their family territories throughout their summer of birth and over winter. Over 57% of juveniles remained in their natal family territory as adults. Dispersal occurred just prior to the reproductive season in spring (Wang and Smith 1989), and males were more likely to disperse than females. Median dispersal distance of young males was two territories; females on average moved only one territory (essentially, next door; Dobson et al. 1998). In a multi-year investigation we detected no long-distance dispersal (Dobson et al. 1998).

Mating Systems

The basic mating system in both American and Plateau pikas is monogamy, although this result may be due to very different circumstances. American pika males largely associate with a single female because they cannot control multiple females (as females are widely dispersed across the talus), nor can they control enough habitat to gain access to multiple females. Thus, they are monogamous almost by default, a condition known as facultative monogamy (Smith and Ivins 1984).

On the other hand, Plateau pikas exhibit a range of mating system types in addition to monogamy; males may live in polygynous, polyandrous or polygynandrous families (Liang 1981; Wang and Smith 1989; Dobson et al. 2000; Smith and Dobson 2004). The proportion of mating systems of any given type varies among years. There is no relationship between habitat quality and mating system type; a family burrow system territory could include a polygynous system in 1 year and any of the other mating system types the next. Apparently the mating system established on any family territory is determined by the sex-ratio of overwintered animals modified by the relatively few dispersal movements just prior to the mating season (Smith and Dobson 2004).

Summary

This broad suite of characteristic differences between American and Plateau pikas (Table 1) represents an excellent opportunity to investigate how animals with similar appearance adapt to the very different habitats they occupy. The population dynamics, reproduction, behavior, dispersal characteristics or mating system dynamics have not been investigated in most species of pika. Much work remains to be done before we can have a comprehensive understanding of these traits across the genus *Ochotona*.

Table 1 Comparative characteristics of rock-dwelling and meadow/steppe-dwelling (burrowing) pikas

Characteristic	Rock-dwelling	Burrowing
Litter size	Small (1–6; generally 3)	Large (1–13)
Litters/year	1–2 (normally only one weaned)	3–5 (all weaned)
Reproductive maturity	Yearling	Young of the year
Longevity	Long-lived (up to 6–7 years)	Short-lived (normally 1+ years)
Density	Low (2–15/ha)	High (up to 300/ha)
Variation in density	Relatively constant	Highly Fluctuating
Mating system	Monogamy (facultative, or live in pairs)	Variable (monogamy, polygyny, polyandry)
Territoriality	Single or Pair	Family
Sociality	Asocial	Highly social
Behavioral repertoire	Limited	Complex
Vocal repertoire (if vocal)	Limited	Complex

American Pika Metapopulation Dynamics

Rock-dwelling pikas represent one of the best models for investigation of metapopulation dynamics. Metapopulations are interdependent patches of occupied and unoccupied habitat, thus are integral for describing the dynamics of fragmented populations. An ultimate goal of metapopulation research is to understand these systems sufficiently to be able to predict their behavior and manage for their persistence. Pikas are ideal for these studies because their obligate habitat type, rocks, is often found in discrete patches.

The population of American pikas at Bodie, California, presents a classic example of metapopulation dynamics (Smith 1974b, 1980; Peacock and Smith 1997; Smith and Gilpin 1997; Moilanen et al. 1998; but see Clinchy et al. 2002). At Bodie, small populations of pikas occupy mine tailing patches in a sea of sagebrush. At any one time, about half of the patches are vacant, although each patch is suitable habitat for pikas and we have evidence that all patches have at one time been occupied by pikas. I have studied the pikas at Bodie since 1969 and have conducted censuses of all patches annually for the past 12 years. Key variables in this system are the occupancy of patches (determined using a variety of features including direct sighting of territorial pikas and presence of fresh sign such as green haypiles, scat piles, etc.), patch size, and degree of isolation of each patch (distance to the nearest occupied patch, or patches).

Bodie pikas appear to be in a dynamic equilibrium between extinction of populations primarily on small habitat patches and recolonization from nearby patches (Smith 1974b, 1980; Smith and Gilpin 1997; Moilanen et al. 1998). This process is slow at Bodie because dispersal is so restricted, mainly due to the high temperatures faced by pikas during dispersal (Smith 1974a). Some years are marked with more frequent extinctions, some with more frequent recolonization episodes—but overall these tend to balance (Smith, unpublished data). More important, however, is that the pattern of patch occupancy at Bodie is highly autocorrelated; a neighborhood analysis indicates that most patches were strongly influenced by the average level of occupancy in surrounding patches. Thus, entire neighborhoods rather than distance to a single potential source patch appear most important in determining the probability of patch occupancy. When the number of nearby patches occupied falls below a threshold number, then entire regions may go extinct as has been observed in the southern network of patches at Bodie (Smith and Gilpin 1997). These results are chilling, in that they demonstrate the sensitivity of metapopulations to collapse. One take-home lesson is the challenge for conservation biologists to identify how to determine thresholds in sensitive species below which their metapopulation dynamics may become inherently unstable (Smith and Gilpin 1997).

There are many rock-dwelling pikas that could be studied to further our knowledge of metapopulation systems in other ecosystems. For example, Franken and Hik (2004) have used the metapopulation approach in their studies of the collared pika (*O. collaris*) to gain greater insight of the role of habitat quality on patch dynamics.

The Plateau Pika as a Keystone Species and Ecosystem Engineer

A keystone species is one whose loss from an ecosystem has a disproportionately large effect on other species, and species known as ecosystem engineers provide additional living space or resource opportunities to target species by altering the structure of their environment (Dickman 1999). The plateau pika is both a keystone species and an ecosystem engineer on the alpine meadow of the Qinghai-Xizang plateau (Smith and Foggin 1999; Lai and Smith 2003; Smith and Harris 2004). Plateau pikas:

- provide habitat for endemic species—we have shown that endemic birds such as Hume's groundpecker (*Pseudopodoces humilis*) and several species of snowfinch (*Montifringilla nivalis, Montifringilla adamsi, Pyrgilauda ruficolis, Pyrgilauda tacazanowskii, Pyrgilauda davidiana*) are most common on areas where pikas have not been poisoned; these species nest in pika burrows that collapse after pikas have been eradicated from a region);

- are a source of food for most predators including weasels (*Mustela* spp.), steppe polecats (*Mustela eversmanii*), Pallas' cat (*Felis manul*), snow leopard (*Uncia uncia*), foxes (*Vulpes* spp.), wolf (*Canis lupus*), brown bear (*Ursus arctos*), Saker falcon (*Falco cherrug*), upland buzzard (*Buteo hemilasius*), black-eared kite (*Milvus lineatus*), golden eagle (*Aquila chrysaetos*), goshawk (*Accipiter gentilis*), and little owl (*Athene noctua*);
- increase plant species richness due to disturbance, and
- increase ecosystem function properties (nutrient cycling, prevention of extensive erosion during the heavy monsoonal rains of summer).

These traits ensure maintenance of biodiversity on the plateau as well as providing benefits for human welfare. Unfortunately, plateau pikas have also been viewed as a pest species and up to 208,000 km^2 of the landscape occupied by pikas has been poisoned in an attempt to eradicate them (Fan et al. 1999). This control effort has been ongoing since 1958 and remains a central governmental activity for management of the increasingly degraded pastureland on the plateau.

Should the plateau pika be treated as a keystone species/ecosystem engineer or as a pest in efforts to manage the fragile alpine meadow ecosystem and ensure that its resources can be productive and sustainable for the benefits of Tibetan pastoralists? The answer to this question depends on (1) the extent that science is allowed to play a role in formulating environmental and development policy; (2) the development of thorough cost/benefit analyses of scenarios (long and short-term) that involve poisoning pikas or allowing them to persist, and; (3) a clear statement of objectives for effective management of the pastureland. Continuing work to understand more completely the ecological role of plateau pikas, in particular their contribution to ecosystem services, is underway in an attempt to shed more light on these issues.

Other pika species have been targeted as pests and poisoned: the Afghan pika (*O. rufescens*), Daurian pika (*O. dauurica*), and Pallas' pika (*O. pallasi*; Smith et al. 1990). In addition, there are many other burrowing meadow/steppe-dwelling pikas that potentially play similar ecological roles throughout their range (Komonen et al. 2003). It is important that studies be initiated on these forms to further our understanding of the overall ecological importance of the genus *Ochotona*.

Conservation Issues

Many pikas are highly endangered due to habitat loss, poisoning, climate change, stochastic metapopulation dynamics, and more. We need to identify those species that are threatened with extinction, to determine the causes, and to formulate a proactive conservation agenda to ensure their continued survival. Some current examples of threats to pika species (Chapman et al. 1990; Formozov 1997; IUCN 2005; IUCN Red List Criteria Ver 2.3 1994 in parentheses) include:

- Koslov's pika (*O. koslowi*) (EN B1 + 2abd): a steppe-dwelling species that is extremely rare and has a restricted geographic range that may be subject to encroaching agriculture and/or poisoning.
- Steppe pika (*Ochotona pusilla*) (VU A1cd, C2a): this species is vulnerable to habitat destruction. In historical times, the Steppe pika has retreated as its habitat was plowed under (Formozov, personal comm.).
- Hoffmann's pika (*Ochotona hoffmanni*) (VU D2), and the Silver pika (*Ochotona argentata*) (CR A2cd): these rock-dwelling forms are known only from extremely restricted areas and are vulnerable to chance extinction—particularly if any anthropogenic force further reduces their ranges or populations.
- Ili pika (*O. iliensis*) (VU D1+2): this cliff-dwelling species that is restricted to two branches of the Tian Shan mountains in China has declined precipitously in the past decade, and this decline may have been caused in part by the effects of global warming (Smith et al. 2004; Li and Smith 2005).

In addition, many subspecies of pikas have been identified as threatened (IUCN 2005). Beever et al. (2003) have determined that over a quarter of known isolated populations of the American pika in the intermountain west of North America have become extinct within the past few decades, a decline that they attribute in part to global warming. Almost all the habitat once occupied by the Indian population of the Moupin pika (*O. thibetana sikimaria*) has been destroyed, making this subspecies critically endangered. Due to the remote localities occupied by many pika species and populations, there are likely to be additional forms that are similarly threatened.

It is incumbent upon us to learn more of the current status of these interesting animals, to study them, and to determine accurately their correct systematic classification. I have outlined several avenues of exciting and important research using two pika species as my prime examples, but little is known about most of the other species. Pikas are also becoming increasingly well known and popular with ecotourists. The Pika Fan Club of Japan, for example, uses the Northern pika (*O. hyperborea*) as a model for ecotourism, and this approach has led to the protection of large tracts of land that had been targeted for development (Ichikawa 1999). I hope that there will be a resurgence of interest in pikas along all of these dimensions, and that at the next World Lagomorph Conference we can look forward to a balanced representation of studies on these wonderful animals.

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