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# Rodent–Pika Parasite Spillover in Western North America

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## Abstract

Competition during the Cenozoic expansion of the Rodentia may have contributed to ecological niche reduction of pikas, which are now increasingly under threat as their habitat degrades under global climate change, while some rodents expand their ranges and overlap with pikas. Range overlap carries the possibility of disease spillover. Contemporary North American pikas are cold-adapted and relegated primarily to alpine environments where they subsist on relatively low-quality herbaceous diet. Yet their evolutionary ancestors were distributed geographically even into the subtropics. Here we examine historical and contemporary records of fleas on pikas (*Ochotona princeps*) from sites at different elevations in the Sierra Nevada and Rocky Mountains and the Pacific Northwest. We calculated indices of diversity from each site and spillover fraction, i.e., the proportion of fleas on pikas that have a preference for rodents. Across this range there are four pika specialist flea species, with no more than two of these per site, and 18 characteristically rodent flea species. Diversity is greatest in the Pacific Northwest and lowest in Montana. Rodent flea spillover onto pikas declines with elevation in the Rocky Mountains. These data provide evidence that rodents and pikas interact enough to allow considerable parasite spillover, and which could be exacerbated as pikas are increasingly stressed by climate change at lower elevations some rodent species expand up-elevation in the face of increasing global warming. With global climate change, both biotic and abiotic niche shrinkage demand our attention.

**Key words:** flea, parasite, spillover, climate change

North American pikas, *Ochotona princeps* and *O. collaris*, live mainly in alpine metapopulations where a typical patch of pika habitat is a rocky "block field" or talus slope (Moilanen et al. 1998, Franken and Hik 2004). The North American pika niche is characterized by access to both rocky shelter and food plants. This ecotone is patchily distributed in western North America, with pikas usually excluded from lower elevation habitats at lower latitudes (Galbreath et al. 2009, 2010). Contemporary pikas are cold-adapted and North American species are considered to be under threat as global warming gradually shifts their already patchy habitat higher in elevation (Hafner 1993, Moritz et al. 2008, Millar and Westfall 2010). Grayson calculates that the average Great Basin pika population has experienced a 783-meter elevation increase over the past 40,000 years as the last glacial period waned (Grayson 2005). At the same time, advancing climate change may promote expansion of ranges of particularly weedy rodents into previously less amenable habitat used by high-elevation pikas (Moritz et al. 2008). Climate-mediated stressors experienced by pikas at lower elevations, coupled with upslope expansion of rodent ranges, might combine to increase the potential for climate-induced competitive interactions between pikas and rodents.

North American pikas showed much greater niche diversity in the Miocene (as did Old World pikas), including, e.g., *Hesperolagomys*, which apparently required closed riparian habitat (Bair 2011). However, worldwide pika diversity collapsed to a single genus during the mid-Miocene through the Pleistocene; at the same time, rodents underwent an extraordinary adaptive radiation, and now comprise about 2,300 species or 40% of all mammal species (Fabre et al. 2012). Contemporary rodents exploit multiple pika resources, and the spatial overlap of pika–rodent territories may be common; e.g., some signs of woodrat presence correlated positively with pika site use across one National Monument in northern California (Ray et al. 2016). Rodents may steal food from pika food caches (haystacks) and behave agonistically toward pikas (Orr 1977). Pikas tend to eat alpine and steppe vegetation, which include many perennial herbs and shrubs whose reproductive strategies rely more on vegetative spread and regeneration than seed production, comprising forage with much less nutritional value than many rodents require. However, lagomorphs and pikas in particular have evolved the ability to exploit this less nutritious vegetation diet by developing hind gut fermentation and coprophagy, the redigestion of caecal feces. The ability to exploit such vegetation largely

differentiates pika niches from the niches of rodents. Pikas also differentiated their niches in their tolerance of cold, contracting their range and species diversity, and retreating up-slope. Where the Miocene featured widespread species across much of North America and many warm habitats, today there are only two species. These two species remain active year-round even where they occur in alpine environments by sheltering under snow in winter and exploiting their stored food caches (Galbreath et al. 2009, Lanier and Olson 2009).

We suspect that apparent competition due to shared parasites is an important form of competition between pikas and rodents. The high diversity and number of rodents sharing space with pikas offers a great opportunity for parasites to spillover from rodents to pikas. While many parasites, such as lice, are highly host-specific, some parasite taxa, such as fleas, feature both specialist and more generalist species. In this paper, we document siphonapteran parasite overlap between western North American pikas and rodents to evaluate the potential for a climate-mediated rise in spillover in disease between pikas and rodents. We conclude that the susceptibility of pikas to rodent parasites, combined with a climate-mediated rise in pika–rodent contact, might adversely affect pika conservation.

There is at present, relatively little data on pika fleas in North America, partly due to the difficulty in capturing pikas for study. This kind of pika research usually requires backpacking at high altitudes and labor-intensive efforts in cleverly placing traps. We augment our own Rocky Mountain pika flea collections with data from two earlier siphonapterists to make available essentially all of the available *Ochotona princeps* flea information. Despite the paucity of pika flea research, rodent fleas, even higher elevation rodent fleas, are relatively well-known compared to other parasitic groups, so that spillover can be readily recognized, and it is often possible to identify the rodent taxon source. Our study shows the extent of such spillover and shows the effect of region and elevation on the spillover.

## Materials and Methods

Flea records were drawn from two sources: published literature and our collections from pikas in Colorado and Montana over the past 10 yr. The two published extensive records of fleas on pikas are Hubbard's long-term collections during the 1930s and 1940s in the Pacific Northwest, and Augustson's Sierra Nevada collections from the same time period (Hubbard 1941, Augustson 1942). Western insect museum flea collections were heavily weighted toward the published collections from Hubbard and Augustson and could only contribute 10 additional pika fleas, nine from three California sites and one from Colorado, which were too few to be statistically analyzed.

Our Rocky Mountain pika fleas were collected during 2005–2014 from alpine and subalpine sites in Gallatin County, MT, and Boulder County, CO (Table 1). Pikas were captured using Tomahawk live traps (Hazelhurst, WI) provisioned with local vegetation and lodged into rock crevices. All work with pikas was performed under the authority of office of the attending veterinarian at University of Colorado-Boulder with permission from the university's Institutional Animal Care and Use Committee, as well as scientific collecting permits approved by the Montana Department of Fish, Wildlife and Parks and Colorado Parks and Wildlife. Pikas were coaxed from traps into a clear plastic chamber and anesthetized with isoflurane. Once nonresponsive and recumbent, the pika was removed from the handling chamber for procedures including examination for fleas. Fleas were also collected directly from the chamber, where they were easily observed during and after exit from a pika's fur.

**Table 1.** Study sites where pika fleas were collected during 2005–2014 from alpine and subalpine sites in Gallatin County, MT, and Boulder County, CO

| Site | State | County | UTM E WGS84 | UTM N WGS84 | Zone | ElevM |
|---|---|---|---|---|---|---|
| Niwot Ridge | CO | Boulder | 449223 | 4434265 | 13 | 3612 |
| Long Lake | CO | Boulder | 449925 | 4435597 | 13 | 3292 |
| Mitchell Lake | CO | Boulder | 449216 | 4437887 | 13 | 3277 |
| Emerald Lake | MT | Gallatin | 505595 | 5028611 | 12 | 2896 |
| Palisade Falls | MT | Gallatin | 505263 | 5035109 | 12 | 2164 |
| Swan Creek | MT | Gallatin | 488238 | 5024548 | 12 | 1829 |

Fleas were stored in 70% ethanol until identification. They were cleared by incubating in dilute KOH for 24 h, then dehydrated in an ethanol series (75, 85, 95, and 100% for 30 min each), and mounted in Euparal (BioQuip, Rancho Dominguez, CA). Fleas were identified using the references and taxonomic keys of Hubbard, Stark, Lewis, and the Rothschild catalogs of the British Museum Fleas (Hubbard 1947, Stark 1958, Hopkins and Rothschild 1971, Lewis et al. 1988, Lewis 2000, Lewis 2002, Lewis and Jameson 2002, Lewis 2009). All flea specimens are presently housed in Dr. Janet Foley's lab at UCDavis and will eventually be transferred to the Bohart Insect Museum.

Flea records were recorded in MSExcel (Microsoft, Redmond, WA) and statistical tests performed using R (R Development Core Team 2008). We define the spillover fraction (SF) as the fraction of flea individuals found on pikas that belong to species normally infesting rodents. We regressed SF on elevation separately for Rocky Mountains and Sierra Nevada using linear regression. Since spillover fraction cannot be perfectly normally distributed (and because our sites vary in sample size), we also ran a generalized linear model (assuming the binomial distribution, i.e., spillover flea versus specialized flea). These analyses used respectively lm() and glm (family = binomial) from the base R package. Ecological diversity measures included richness, Simpson's inverse measure of diversity, the exponent of the Shannon–Wiener diversity measure, and evenness following formulas in (Krebs 1999). "Preferred hosts" were defined simply as the host species or genus reported by Hubbard as preferred for that flea species.

## Results

Four North American flea species specialize on pikas: *Geusibia ashcrafti* and *Ctenophyllus armatus terribilis* of the family Ctenophthalmidae, and *Amaradix bitterrootensis* and *Amphalius necopinus* of the family Ceratophyllidae. Eighteen rodent-specialist flea species spill over onto pikas, mostly from the family Ceratophyllidae. Table 2 contains a summary of the fleas reported in the two published West Coast studies together with our new results from Colorado and Montana. Flea spillover appears to come from a diversity of rodents: of those rodent fleas found on pikas, 27.8% were reported to have a preference for woodrats, 16.7% each for chipmunks, ground squirrels, and deer mice, 11.1% for tree squirrels, and 5.6% each for voles and marmots. One species, *Rhadinopsylla fraterna*, is reported to be a generalist of various rodents.

**Table 2.** North American pika fleas

| Flea species | Preferred host | PNW | SN | CO | MT |
|---|---|---|---|---|---|
| *Geusibia ashcrafti* | *Ochotona princeps* | | 43 | | |
| *Ctenophyllus armatus terribilis* | *Ochotona princeps* | 14 | | 181 | 24 |
| *Amaradix bitterrootensis* | *Ochotona princeps* | 30 | | 1 | |
| *Amphalius necopinus* | *Ochotona princeps* | | 19 | 73 | 2 |
| *Peromyscopsylla ravalliensis* | *Neotoma* | | | 1 | |
| *Aetheca wagneri* | *Peromyscus* | 4 | 5 | 6 | 1 |
| *Ceratophyllus ciliatus protinus* | *Tamias* | 2 | | | |
| *Eumolpianus cyrturus* | *Tamias* | 2 | | | |
| *Eumolpianus eumolpi eumolpi* | *Tamias* | | | 1 | |
| *Megabothris abantis* | *Microtus* | 8 | | 7 | 7 |
| *Megarthroglossus divisus exsecatus* | *Neotoma* | | | 1 | |
| *Megarthroglossus procus* | *Tamiasciurus* | | 10 | | |
| *Orchopeas nepos* | *Tamiasciurus/Sciurus* | 1 | 1 | | |
| *Orchopeas sexdentatus agilis* | *Neotoma* | 17 | | | |
| *Orchopeas* near *sexdentatus* | *Neotoma* | | | | 2 |
| *Oropsylla idahoensis* | *Urospermophilus/ Callospermophilus* | 6 | | | |
| *Oropsylla montana* | *Otospermophilus/ Urospermophilus* | 4 | | 1 | |
| *Phalacropsylla allos* | *Neotoma cinerea* | | 2 | | |
| *Rhadinopsylla fraterna* | Generalist | 1 | | 1 | |
| *Rhadinopsylla goodi* | *Peromyscus* | | | 1 | |
| *Thrassis acamantis howelli* | *Marmota flaviventris* | | 1 | | |
| *Catallagia chamberlini* | *Peromyscus* | 3 | | | |
| Total | | 88 | 85 | 273 | 37 |
| Pika specialist fraction | | 0.5 | 0.729 | 0.933 | 0.703 |
| Rodent flea spillover fraction SF | | 0.5 | 0.271 | 0.067 | 0.297 |
| Spillover diversity, species richness S | | 9 | 6 | 7 | 4 |
| Spillover diversity exp(H) | | 6.36 | 4.41 | 4.65 | 2.81 |
| Spillover diversity, reciprocal Simpson index $S_r$ | | 4.88 | 3.6 | 3.6 | 2.2 |
| Evenness exp(H)/S | | 0.71 | 0.74 | 0.65 | 0.70 |

Pacific Northwest (PNW) fleas were collected by Hubbard before 1941 in Washington, Oregon, and northern California and Sierra Nevada (SN) fleas were collected by Augustson in the central Sierra Nevada (Hubbard 1941, Augustson 1942, Hubbard 1947). Montana and Colorado fleas were collected by Chris Ray and colleagues from 2005 to 2014, reported here for the first time. Spillover fraction SF is the fraction of the fleas found on pikas that are normally believed to prefer rodents. This and the standard diversity measures are explained in the materials and methods.

Rodent flea spillover onto pikas varies across western North America regionally and elevationally. The spillover fraction, SF reaches 0.50 in the Pacific Northwest (where we do not have elevation data on the historical Hubbard collections), whereas SF = 0.268 at intermediate elevations in California's Sierra Nevada, and drops to less than 0.1 at high elevations in the Rocky Mountains of Colorado. At lower elevations in the Rocky Mountains, SF is high (0.297), and more similar to that in the Sierra Nevada, although based on fewer data (37 fleas). Table 3 shows the fleas from pikas and their host preference at six field sites in the Rocky Mountains. Linear regression of these SF on elevation for the Rocky Mountain sites shows an elevational gradient: SF = 0.7884 − 0.0002039 * elevation in meters ($P = 0.002$, $R^2 = 0.927$, $N = 6$). A similar regression is produced from Augustson's Sierra Nevada fleas: SF = 0.7609 − 0.0002041 * elevation, but it is not statistically significant ($P = 0.42$, $R^2 = 0.135$, $N = 6$). Because SF cannot be entirely linear, we also ran a logistic regression. Rocky Mountain SF showed a significant elevation effect under logistic regression also ($P = 0.00003$). The resulting model was

$$\log(\mathrm{SF}/(1 - \mathrm{SF})) = 4.0946 - 0.0019 * \text{elevation (m)}.$$

The elevation at the inflection point or break of the logistic curve, where SF = 0.5, is calculated as 4.0946/0.0019 = 2,155 m for the Rocky Mountain pika fleas. The linear model places the break point at 1,414 m, well below our sites.

The pika specialist flea guild, though not diverse, does vary across sites, with typically only two specialist flea species per site (Table 2). In contrast, the guild of rodent fleas that occasionally infest pikas (the spillover guild) is much more diverse and differs in composition across sites. It is most diverse, by species richness as well as Simpson and Shannon–Wiener indices, in the Pacific Northwest and declines to its lowest diversity in Montana (Table 2). Spillover guild evenness is fairly constant across sites.

## Discussion

Across their range, North American pikas are exposed to fleas and to the pathogens that fleas may transmit. Most fleas collected from pikas are specialists on pikas. However, especially at lower elevations, we found a significant flea burden spilling over from sympatric rodents onto pikas. Fleas are only one taxon out of the many pathogens and parasites which rodents may share with pikas. Further expansion of rodents into previously cold, alpine habitats, mediated by climate change, may cause apparent competition via parasites and disease between rodents and pikas, with expected negative consequences for pika conservation. It is also possible that lower elevation pikas, increasingly stressed by warmer conditions, have become more susceptible to parasites even if rodent-pika interactions have not yet been directly affected by climate change.

Compiling flea records from diverse sources and analyzing diversity patterns statistically was challenging because of spotty coverage,

**Table 3.** Rocky Mountain pika fleas, *Ochotona princeps*, collected by Chris Ray and colleagues from 2005 to 2014

| Flea species | Colorado: Boulder County | | | Montana: Gallatin County | | |
|---|---|---|---|---|---|---|
| | Niwot Ridge | Long Lake | Mitchell Lake | Emerald Lake | Palisade Falls | Swan Creek |
| Elevation (m) | 3,612 | 3,292 | 3,277 | 2,896 | 2,164 | 1,829 |
| *Ct. arm. terribilis* | 107 | 52 | 22 | 20 | 2 | 2 |
| *Ama. bitterrootensis* | | | 1 | | | |
| *Amphalius necopinus* | 29 | 12 | 32 | 1 | | 1 |
| *Peromyscopsyl. ravalliensis* | | 1 | | | | |
| *Aetheca wagneri* | 4 | | 2 | | 1 | |
| *Eumolpianus eumolpi* | | | 1 | | | |
| *Megabothris abantis* | | 4 | 3 | 7 | | |
| *Megarthro. d. exsecatus* | | | 1 | | | |
| *Orchopeas nr sexdentatus* | | | | | | 2 |
| *Oropsylla montana* | | | | 1 | | |
| *Rhadinopsylla fraterna* | | | 1 | | | |
| *Rhadinopsylla goodi* | | 1 | | | | |
| Total | 140 | 70 | 63 | 29 | 3 | 5 |
| Pika specialist fraction | 0.97 | 0.91 | 0.87 | 0.70 | 0.67 | 0.6 |
| Rodent spillover fraction SF | 0.03 | 0.09 | 0.13 | 0.3 | 0.33 | 0.4 |
| Spillover diversity S | 1 | 3 | 5 | 2 | 1 | 2 |

Spillover fraction SF is the fraction of the fleas found on pikas that are normally believed to prefer rodents. This and the standard diversity measures are explained in the materials and methods.

possible confounding, changing taxonomy and differing collection methods. Of course it would be much easier if all sites were sampled in the same way, same time of year, and even same decade but they were not. With respect to seasonality however, samples were all collected when snow was off the site, typically summer. With respect to collection technique, the initial Hubbard and Augustson publications were from the lower elevation and Sierra Nevada fleas on pikas, using shotgun and steel traps in the 1930s and 1940s. Fleas leave dead hosts quickly, possibly accounting for why Hubbard found fewer than one flea per pika host. Although this capture technique may have resulted in low recovery rates of fleas, there is no reason to expect bias in which fleas remained. Chris Ray's contemporary Montana and Colorado Rocky Mountains collections are likely more comprehensive than earlier assessments of fleas on pika individuals, because anesthesia appears to prompt some fleas to leave the host, and these fleas are retained in the anesthetizing chamber. The designation of the "preferred host" for fleas was somewhat subjective, although Hubbard's comprehensive accounts collated data from all of the key flea resources available at the time of his book's publication, and include tens of thousands of flea accessions, suggesting that this indication of preferred host is very good. All collections we examined revealed spillover of rodent fleas onto pikas, particularly from woodrats. However, the highest elevations were associated with lower spillover fraction, whether comparing Rocky Mountains to Sierra Nevada or higher elevation Rocky Mountains to lower elevation Rockies.

Parasite prevalence and load in general can be heterogeneous over space and time due to herd immunity dynamics, but this is unlikely for fleas and other ectoparasites which are minimally affected by the host's adaptive immune system. More likely, the climatic features of the highest elevations minimized rodent-pika interaction and spillover. Possibly, rodent fleas themselves are less fit in dealing with the drier conditions of higher elevations. A recent survey of seven sites (2,180–3,170 m) in the Colorado Front Range did not find a significant relationship between elevation and small mammal flea diversity (Maher and Timm 2014), but our Rocky Mountain pika research includes three sites of higher elevation than the Maher and Timm study.

The evolution of fleas and their pika and rodent hosts represents a complicated long-term interaction, featuring multiple rounds of phylogenetic expansion and geographical spread in ochotonids, followed by the recent, extreme contraction to only the two North American species, in contrast with the dramatic diversification of rodents. Specialized pika fleas appear to have evolved from rodent flea clades. Worldwide, there are dozens of specialized pika fleas from four families of Siphonaptera. The phylogeny of Siphonaptera is only partially understood at present (Whiting et al. 2008), but Whiting's molecular phylogeny suggests that most pika specialist fleas are nested inside rodent flea clades. If this is so, it suggests that parasite spillover from rodents to pikas is an ancient tradition.

Rodentia and Lagomorpha form the clade Glires which split about 61.7 MYA; the earliest Lagomorpha in the fossil record is from 50–60 MYA (Benton and Donoghue 2007). Ochotonidae originated in Asia in the Middle Oligocene (Erbajeva 1994), splitting from the Leporidae (~60 extant species) about 30 MYA or earlier (Timm and Clauson 1985, Lanier and Olson 2009). There were 19 fossil genera and numerous species in the Miocene across Eurasia, Africa, and North America (Erbajeva et al. 2011), and as many as eight lagomorph species could occur in sympatry, including several ochotonids (Lopez-Martinez 2008).

The era of greatest ochotonid diversity was considerably warmer worldwide than today and their previous range of habitats more diverse, with the last non-*Ochotona* genus (*Prolagus*) finally being lost on Sardinia and Corsica during Roman occupation (Prieto et al. 2012). There remain 28 pika species in Asia, comprising solitary alpine talus-dwelling pikas and social, burrowing steppe pikas (Smith 2008), but almost all of the North American diversity was lost by late Miocene. Much later, Pliocene or Pleistocene pikas of the genus *Ochotona* appear to have spread in one or two migrations (Erbajeva et al. 2011) from Beringia to eastern North America and diversified into several species, all but two of which are now extinct (Lanier and Olson 2009).

A recent effort to explain ochotonid decline relies on climate change which increased the ratio of C4 to C3 plants (Ge et al. 2013). While it is true that ochotonids eat more C3 plants than C4 plants, their current diet might simply be enforced by their consignment to colder habitats. That this retreat to colder and harsher habitats is due to competition with rodents is supported by observations of competition for alpine meadow vegetation among pikas, voles, and marmots (Orr 1977). Mountain beavers (*Aplodontia rufa*) have even been observed making haypiles that were similar to pikas' (Orr 1977). Russian pikas share burrows with (and may need to defend food from) a diversity of rodents including voles, marmots, and jerboas (Sokolov et al. 2009). It is ironic that so many explanations for limited ochotonid distribution invoke a requirement for limited, colder, higher altitude habitats, while the fossil record clearly demonstrates that ancient pikas were well-adapted to warmer climates (Bair 2011). It has even been suggested that the extant isolated, low-elevation colonies, for example in Lava Beds National Monument, may be remnants from a more successful, warmer Pleistocene distribution (Orr 1977).

Disease and parasites are under-studied stressors on pika health and local and regional pika persistence (Ray et al. 2012, Wilkening et al. 2011). Some disease ecology theory predicts that parasites have less effect on endangered, compared with common, hosts because specialist parasites are likely to go extinct before their hosts. In contrast, in just these dwindling host populations, generalist parasites or parasite spillover from abundant alternative hosts play a dangerous role (Woodroffe and Ginsberg 1998, Foley and Foley 2012). And it is exactly in metapopulations that small fitness effects of parasite load can have their most nonlinear, damaging results (Foley and Foley 2012). Even without invoking the subtleties of nonlinear dynamics, the effect of parasites on pika populations can be profound. Sylvatic plague caused by the flea-transmitted bacterium *Yersinia pestis* often affects Asian pika populations (Biggins and Kosoy 2001). *Ochotona mongolica* and *O. dauurica* experienced an epizootic in 1959 following a 1958 epizootic in the vole *Alticola* (Shchekunova et al. 1964). The Ili pika (*O. iliensis*) has recently been sampled at 14 previously occupied sites in the Tian Shan mountains of western China, but no pikas were captured or observed, and in 8 of the sites, no fresh pika sign was found (Li and Smith 2005). The authors did not definitively determine the cause of the decline, but suggested these possible causes: climate change, livestock disturbance, and plague transmitted from *Marmota baibacina*. Since its introduction in North America around 1900, plague has altered North American mammal communities dramatically through mass epidemics among ground squirrels, prairie dogs, and other species (Gage and Kosoy 2005). Plague persistence and emergence in North America have been associated with meteorological conditions (Parmenter et al. 1999, Snäll et al. 2008), and plague is hypothesized to play a role in North American pika extirpations (Wilkening et al. 2011).

There are a number of other diseases that may regulate pika populations and could contribute to apparent competition with rodents. The agent of "rabbit fever", *Francisella tularensis*, which occurs in numerous small mammal species, may be a risk for pikas, although there is little work regarding this pathogen (Busoedova et al. 1982). Chinese populations of *O. curzoniae* are thought to be partially regulated by a consortium of parasites including the flea *Pulex* sp., the bot fly *Hypoderma curzonial*, the tick *Ixodes ovatus*, and the pinworm *Cephaluris coloradensis* (Wang et al. 2009). At one site in Colorado, pika intestines were obstructed by unidentified tapeworms (Martin 1943), and a large tapeworm was observed in the caecal feces of a Colorado pika in 2012 (J. Wilkening, personal observation). Of the nematode parasites of pikas, several are plausibly plesiomorphic to Lagomorpha. The pika roundworm *Graphidiella* is in the trichostrongylid subfamily Graphidinae which includes leporid, suid, and bovid roundworms (Anderson 2000). A plausible source for transmission of sympatric small mammal gastro-intestinal parasites to pikas is via feces; for example North American pikas cache marmot feces within their food stores or "haystacks" (Orr 1977). Although leporid lagomorphs have been successfully infested with rodent and ungulate nematode parasites, the one experimental inoculation of *Ochotona* with *Heligmosomoides laevis* did not result in infestation (Audebert and Durette-Desset 2007). Nevertheless, it is plausible that other parasites do cross species boundaries to infect pikas. Additional studies could for example evaluate possibly shared gastrointestinal parasites through examination of fecal and caecal pellets, which can be collected noninvasively.

The paleontological record and the parasite spillover evidence suggest that modern pikas, which indeed persist in cold, harsh habitats, do so in part as a result of competitive exclusion by rodents. While climate change will have some direct effect on these cold-adapted pikas, the ultimate challenge they may have to face will be associated with the effects climate change has on their rodent competitors and perhaps on the parasites they carry. Regional surveys have been undertaken in the past decade in the western U.S. to evaluate potential changes in the pika's status (Jeffress et al. 2013). If competition with rodents is playing an important role in pika decline, we should monitor these competitors. If parasite spillover is mediating apparent competition, then more attention should be paid to pika parasites. Where climate change is affecting rodent distributions and parasite spillover, then appropriate data and predictive models are needed to quantify and then mitigate these effects. Even if ectoparasite spillover plays little direct role in pika fitness, such spillover may be a useful tool to measure the level of rodent–pika interaction. Through direct observation of rodent range expansion (Moritz et al. 2008) and pika range contraction (Beever et al. 2011), coupled with evidence of parasite spillover that we provide here, a better picture of pika risk due to changing climate emerges.

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