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Distribution and Climatic Relationships of the American Pika (*Ochotona princeps*) in the Sierra Nevada and Western Great Basin, U.S.A.; Periglacial Landforms as Refugia in Warming Climates. Reply

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We thank Dr. Wolf and the Editor of AAAR for an opportunity to further discuss the status of American pika (*Ochotona princeps*) in western North America. We address the two main points of Wolf, namely that our surveys do not warrant conclusions that (1) “pikas appear to be thriving in the Sierra Nevada (SN) and southwestern Great Basin (swGB),” and that, (2) pikas are “tolerating a wide range of thermal environments.”

1. Pikas appear to be thriving in the Sierra Nevada and southwestern Great Basin

Wolf's first criticism (2010) questions the value of spatially extensive, presence/absence surveys such as ours rather than repeat monitoring of historic records from specific locations. We presented our approach explicitly as a rapid assessment method for assessing geographic extent of pika habitat and noted that such methods are best used in conjunction with trend analyses: “This [rapid assessment] approach complements and should not replace intensive transect- and plot assessments or repeat surveys of historic populations. The latter are essential for basic species understanding but are limited in geographic coverage due to the effort required” (Millar and Westfall, 2010, p. 86).

Repeat monitoring has greatest value when inventories are made regularly over many decades, such as has been done in the pioneering work of Andrew Smith at Bodie, California (Smith, 1980). As demonstrated by Smith's cumulative results, pika populations fluctuate dramatically in frequency of extirpations versus colonizations from year to year. Nearly annual censuses of pikas that occupy a suite of ore dumps at Bodie State Historic Park—the lowest and hottest area where pikas have been continually observed—show that extinctions of populations on ore dump patches and subsequent recolonizations of unoccupied ore dumps vary significantly from year to year. Some years are characterized by many patch extinctions, and others by frequent recolonizations. The overall number of extinctions and colonizations has been nearly equal over this span of years, demonstrating the equilibrium nature of these dynamics at Bodie (Andrew Smith, personal communication, 2010; see figures in Millar et al., 2010a). Trends interpolated from two or several points mean little about long-term status. This is expected for pikas, which define textbook metapopulation dynamics and are expected to undergo repeated

patch extinctions and recolonizations (Gilpin and Hanski, 1991; Smith and Gilpin, 1997). Even after three decades of monitoring at Bodie, detection of any directional trends is uncertain, let alone attribution of any trend to forcing factors (Andrew Smith, personal communication, 2009). Wolf cites a dictionary definition for thriving that fails to acknowledge these basic animal population dynamics: If a population is at carrying capacity, it cannot exhibit growth; a metapopulation species will undergo extirpations as part of healthy fluctuations.

Such caution as learned at Bodie, implicit from metapopulation dynamics, must extend to interpretations of repeat surveys at sites such as early 20th-century locations in the Great Basin (e.g., Beever et al., 2003). Here again, two points do not make a trend, as highlighted by Beever et al. (2010), wherein one of the populations (Cougar Peak, Oregon), scored during their 1994–1999 surveys as “functionally extirpated,” was observed in 2005–2007 to “host a robust population.” In June 2010 we revisited several of the same historic locations in the northern Great Basin and also found Cougar Peak to have extensive pika occupation. In a single day's survey, we made pika sightings and vocalizations extending from taluses at 1928 m to the summit of Cougar Peak (2414 m), and on all aspects of the mountain. Although we visited during midday (the time of day least optimal for observing pika activity), we heard and saw many pika and found abundant evidence of current occupation (fresh haypiles, pellets, and urine posts). Our observations make it curious that Beever et al. (2010) wrote, in regard to their prior finding of functional extirpation, “This discrepancy [from functionally extirpated to robust population] was likely due to insufficient sampling, rather than increased density: during the 1990s; Cougar Peak was not visited during times of day optimal for observing pika activity.”

In 2010 we also revisited the early 20th-century record pika location at Summit Lake, Nevada. This site is highly disjunct from other pika taluses, and has very limited pika habitat at the site. It was scored as extinct in 1994–1999 and 2005–2007 surveys (Beever et al., 2003, 2010). Although we did not see or hear pikas in a single mid-day survey, we did find fresh haypiles, fresh pellets, and fresh urine posts, indicating that this location might have recolonized and should be resurveyed again before the metapopulation is determined to be extirpated.

These examples demonstrate the challenges in interpreting time-series surveys and especially the pitfalls of concluding

directional trend (e.g., “declining”) or status (e.g., “extirpated”) in a metapopulation species. The significant challenges in animal species more generally of detecting and attributing trends from repeat censuses have led to development of spatially extensive presence/absence occupancy methods as alternatives to temporally intensive methods. These evaluate population occupancy across wide ranges of environments as a means to investigate population status (e.g., MacKenzie et al., 2003, 2006). Our rapid-assessment methods, which record pika-presence as well as pika-absence sites, approximate the rigorous approaches of such occupancy modeling. Further, habitat-based (e.g., talus), spatially extensive point surveys such as ours that use indirect as well as direct sign parallel those described in established protocols for pikas (Ministry of Environment, Lands, and Parks, 1998; USDI National Park Service, 2010) and for another patchily distributed western lagomorph, pygmy rabbit (*Brachylagus idahoensis*; Ulmschneider, 2004; Hagar and Lienkaemper, 2007; Himes and Drohan, 2007; Larrucea and Brussard, 2008a).

Wolf asserts that our sites were “haphazardly selected”, implying perhaps that they are biased locations. The established protocols cited above describe a similar approach for opportunistic searching at the landscape scale as we did. Our observations focused initially on prime habitat (alpine elevations, talus with optimal clast size, abundant forefield herbaceous vegetation) but we soon extended into elevations and habitats considered less optimal, thus exploring the margins of habitat use. Eventually this took us to locations and environmental conditions beyond pika habitat and allowed us to assess differences between habitats currently used by pika and those not used. Our 420 published sites (expanded to 587 locations during the time since publication) extended over 2060 m of elevation, included 11 mountain ranges, included 10 geomorphic habitat categories, were observed on all slope aspects and slope inclinations, and included diverse substrate types occurring in the environments of investigation. Overall, this large number of sites over a wide range of environments provides a robust opportunity for exploring the geomorphic and climatic elements of site use by pikas in our region.

The large number of sites in our study, extending across broad ranges of elevation and extending from optimal to less preferred habitat, provides a more robust opportunity to explore regional habitat uses of pikas than studies focusing on a small number of sites. The 25 historic locations Wolf notes as being revisited in the Great Basin, for example, are an extremely limited representation of the extensive Great Basin landscape. In our recent visits to early 20th-century pika sites from the northern Great Basin (Oregon and Nevada) of Verts and Carraway (1998) and Hall (1946), we found many of these to be a very odd set of pika sites from the standpoint of typical (e.g., as described by Smith and Weston, 1990) habitat. It appears that they most likely represent pika records gathered for reasons other than for systematic pika surveys (e.g., locations are at a fire lookout, a U.S. Forest Service guard station, a game refuge). Several of these locations are extremely small and marginal pika habitat compared to typical habitat, and highly disjunct from continuous habitat that exists in many high Great Basin ranges. Whereas these remote sites would make excellent focus for studies of rare dispersal potential, maintenance of populations in disjunct locations, or effects of inbreeding in small isolated patches, they are a poor set of sites for interpreting pikas’ persistence across representative habitat of the Great Basin. When we revisited more typical pika locations recorded from the historic literature for the Great Basin (e.g., Hart Mt, Warner Mt, Toiyabe Mtns, Toiyama Mtns, White Pine Mtns), we found evidence of pika occupancy.

Wolf further questions whether we accurately scored site ages. The pika and pygmy rabbit protocols cited above all specify the value and use of indirect sign and their interpretations for occupancy. A recent meeting of the California Pika Consortium (CPC, 1 July 2010, Sacramento, California; <http://www.dfg.ca.gov/wildlife/nongame/CPC/meetings/2010-07-01.html>) on monitoring methods addressed this question directly. Visual and aural observations were agreed to be the most certain sign of pika presence, although even in occupied habitat and at appropriate times of the day pikas are often not active on the talus surface or vocalizing. Green vegetation in haypiles, in association with other indirect sign (pellets, urine posts), was widely trusted to indicate active use, given that *Neotoma* is ruled out as having taken over pika haypiles, and recognizing that in many locations haypiles are not found at all (Beever et al., 2008; Ray and Beever, 2007; participants at CPC meeting). Early in the summer before haying has begun (mid- to late August in the SN and swGB) there is no or little green vegetation in haypiles and age of indirect sign relies on interpretation of vegetation in haypiles and assessing age of pellets and urine. Pika researchers at the CPC meeting agreed that co-occurrence of several types of fresh indirect sign rather than one type alone provides improved evidence for interpreting a site as modern, although occupancy cannot be considered definitive.

Our observations in early spring of known active pika sites in the SN and swGB ranges indicate that pellet signs are not long-lasting and indicate recent occupation. Pellets washed away from all talus locations revisited except haypile sites, and pellets in haypiles turned from green and soft (fresh) to brown and starting to decompose. Recognizing that direct and indirect signs have different levels of confidence in scoring a site as active, we specifically kept these categories separate in our 2010 report. There is no reason *a priori* to assume, as Wolf implies, that these are not active sites.

Wolf’s comment that pika pellets are able to persist for millennia as indicated by Grayson (2005) from Pleistocene and Holocene archeological and cave sites is not relevant for documenting longevity of pellets in native pika habitats or conditions. Pika pellets cited by Grayson were recovered from woodrat (*Neotoma* spp.) middens (Thompson and Mead, 1982; Mead and Spaulding, 1995; Rhode and Madsen, 1995) and as such were preserved in amberat, which seals and protects organic material against degradation from atmosphere and water in the same manner in which museum archives protect specimens for millennia.

Wolf questions whether the environmental range of sites in our study exceeds historic description, a finding that we used to demonstrate pika current status. While Wolf’s criticism in itself seems like a statement for the health of modern pikas (i.e., current diversity is equal to historic diversity) the historic record we cite indicates narrower range limits than we found in our study. Such quotes as Wolf cites (“widely distributed,” “abundant,” “a common resident,” “one cony per 750 square yards”) provide no information on species or subspecies range width or diversity. The literature we cited, by contrast, gives explicit values for elevation margins in the different mountain ranges and subspecies of our study region. Using these records rather than anecdotal notes about abundance indicates that our range of sites is wider than the early literature describes.

Wolf questions our basic unit of analysis, the site occurrence (site), which we limit to a single pika home range, or minimum of 50 m separating sites. We adopted this from the literature to exceed the largest nearest-neighbor distance and home-range diameter for pikas (Smith and Weston, 1990, p. 78; Beever et al., 2008). We subsequently grouped sites into demes, again using the

literature-based estimate for maximum dispersal of individual animals (3 km; Smith and Weston, 1990), and grouped demes into geographic regions and these into mountain ranges. For all cases, thus, we follow maximum distance estimates from the literature to improve the likelihood that our site occurrences represent individual pikas and do not overcount animals. Our basic unit is larger than that used in draft National Park Service protocol, which uses a 24 m diameter plot (USDI National Park Service, 2010). Our method does not amount to pseudo-replication, as Wolf asserts, whereby single sites are repeatedly sampled, but cluster (or hierarchical) sampling or classification, a standard method in population genetic sampling (Weir, 1996).

By defining individual sites in this way, we leave no question about the exact location for each of our records, a problem that has plagued other papers about pikas, where notation is unclear as to whether an observation refers to a talus patch, a group of patches, or an entire mountain range. Given the size rule for our basic unit, other researchers can readily group our site occurrences into geographic clusters of value to their analytic purposes or geographic domains.

Documentation of a species occupying its historic range and extending beyond historic limits is commonly used as an indication of a healthy, thriving wildlife species, for example, for pikas (Beever, 2002; Ray and Beever, 2007; Beever et al., 2008; Simpson, 2009), related pygmy rabbits (Himes and Drohan, 2007; Larrucea and Brussard, 2008b), and more generally (e.g., Link et al., 1994). Our conclusion of pikas' population viability in our region parallels these interpretations.

2. Pikas are tolerating a wide range of thermal environments

Wolf (2010) questions the validity of using surface air temperatures (modeled by PRISM) across pika sites to indicate a range of thermal environments experienced by pikas, claiming that internal talus temperatures are more important to pikas than air temperatures. This is an odd argument for two reasons. First, the petitions to list pika as endangered, authored by Wolf, repeatedly use projected warming of *surface* air temperatures as primary evidence that pikas are at risk across their range from global warming (Wolf et al., 2007a, 2007b). The petitions cite models of increasing surface air temperature at both global scales (IPCC projections; Meehl et al., 2007) and in regionally downscaled climate projections (Snyder et al., 2002; Loarie et al., submitted) to document the threat of air temperature increases to pika persistence. Given the significance that future air temperatures have been given in the literature to forecast risk to pikas, we felt it was important to document observed ranges of air temperatures at our pika sites.

Furthermore, the scale of the PRISM tiles used in Loarie et al. (submitted) is modeled at coarse resolution and can include areas hundreds of meters from the tile elevation. We used data from the downscaled PRISM data and adjusted data by the difference between the PRISM tile and the elevation of the site using the estimated lapse rate of the respective PRISM tile.

Second, Wolf's claim that internal talus temperatures are likely more important to pikas than air temperature is odd because this is exactly the argument we make in our paper. Our lengthy discussion of periglacial rock-ice features (RIFs) and their little-explored thermal regimes (p. 84ff; section titled, "Topographic-Climatic Conditions and Intra-RIF Microclimates") is based on our previous investigations of RIFs in the Sierra Nevada (Millar and Westfall, 2008). Whereas we presented instrumentally

measured observations for only five pika RIF sites in Millar and Westfall (2010), we have compiled a larger database of other RIFs (many are pika habitat) in the SN. Cumulative results from these records indicate internal talus-matrix environments to average much cooler than summer surface air temperature and having temperatures highly attenuated relative to diurnal fluctuations in surface air temperature (Millar and Westfall, unpublished). Although internal thermal environments of RIFs are beginning to be studied in Arctic environments and the European Alps (citations in Millar and Westfall, 2008, 2010), they have been little investigated in North America. In Millar and Westfall (2010) we encouraged research to address this critical element of pikas' habitat.

In light of this need we initiated an intensive study in 2009 of internal thermal regimes of pika taluses, wherein we deployed thermochrons to measure surface- versus rock-matrix temperatures at pika taluses for low and high elevation sites in the Sierra Nevada. We reported the first summer observations at CPC- and The Wildlife Society-sponsored technical sessions in fall 2009, and our first winter records at the MtnClim 2010 conference (Millar et al., 2010b). This study is corroborating early indications that internal talus thermal regimes, combined with behavioral adaptations of pikas (Smith, 1974) provide microclimatic conditions that enable pikas to occupy habitats over wide ranges of environments and surface air temperatures such as in our study.

Wolf challenges that our estimates of surface air temperature do not demonstrate a wider range of temperatures than has been published in previous literature and thus do not warrant a conclusion that pika are occupying a broader range of environments. A careful reading of Millar and Westfall (2010, pp. 83–84), however, indicates our estimated climatic range to extend beyond the published estimates available for pika. We noted this as especially indicative of pikas' current capacity, given that the published values we cited were for the range of pika across western North America, whereas even in the limited portion of the range we found that pikas sites extending beyond these values.

Finally it is odd that Wolf would argue for the importance of internal talus temperatures and the lack of importance of surface air temperature yet conclude her response (final sentence) by citing the importance of surface air temperatures projections (Galbreath et al., 2009).

In sum, we maintain that the range of pika sites over diverse environments and extending beyond published historic records and climates provides strong evidence for pika population persistence and accommodation of considerable climatic diversity in our study region.

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