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PATTERNS OF APPARENT EXTIRPATION AMONG ISOLATED POPULATIONS OF PIKAS (*OCHOTONA PRINCEPS*) IN THE GREAT BASIN

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?1 We conducted exploratory analyses to examine the relative roles played by natural and anthropogenic influences on persistence of a montane mammal. We revisited historical locations of pikas (*Ochotona princeps*) within the hydrographic Great Basin during summers of 1994–1999. Seven of 25 populations (28%) reported earlier in the 20th century appeared to have experienced recent extirpations. We assessed causative agents of faunal change using several alternative, but not mutually exclusive, hypotheses. Higher probability of persistence was correlated with greater area of talus habitat at local and mountain-range scales, higher elevation, more easterly longitude, more southern latitude, lack of livestock grazing, greater distance to primary roads, and wilderness management. However, only area of habitat in the mountain range, maximum elevation of talus habitat, and distance to primary roads appeared in the most parsimonious model of persistence when we used Akaike's information criterion model-selection technique. These results suggest that relaxation of montane faunas may occur more rapidly than previously expected; that biogeographic models of species occurrence can be refined by including more proximate factors (e.g., grazing status, proximity to roads); and that habitat-based approaches to modelling vertebrate trends should be accompanied by field data because population loss can occur with no apparent change in habitat.
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Key words: American pika, biogeography, climatic effects, extinction, grazing, hydrographic Great Basin, land management, montane alpine habitat, *Ochotona princeps*

Persistence of animals in heterogeneous landscapes may vary as a result of habitat complexity or quality (Johnson 1975; Pulliam 1988), initial population size (Newmark 1995; Pimm et al. 1988), spatial arrangement of patches and dispersal frequency (Hanski 1991, 1998), frequency of and response to catastrophes (Mangel and Tier 1994), and life-history characteristics of species (Newmark 1995; Tracy and George 1992). Few studies have assessed the rela-

tive contributions of natural and current anthropogenic factors to risk of extinction, and those that have done this have often examined broad taxonomic groups (Ceballos and Brown 1995; Cole et al. 1994; Kerr and Currie 1995; Newmark 1995) or lacked recent empirical data on population trends (e.g., Ceballos and Brown 1995). A taxonomically coarse-scaled approach provides a summary of factors most frequently acting on species within a clade; however, it does not allow an in-depth examination of extinction dynamics (e.g., interactions of

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several threats). We attempted to investigate persistence of a discontinuously distributed mammal species in relation to biogeographic, climatic, and current anthropogenic factors.

Isolated mountaintops in western North America have been considered montane habitat islands, and patterns of species occurrence have been investigated in birds, butterflies, conifers, and mammals of the Great Basin, as well as in montane mammals of New Mexico (e.g., Brown 1971, 1978; Cutler 1991; Johnson 1975). Although montane mammal fauna of the Great Basin have been used as models to examine biogeographic patterns for nearly 3 decades, there is no clear consensus on factors that most strongly influence persistence in these communities. Island area, degree of isolation from local colonizing sources and mainland habitat, and habitat diversity have been assessed, but it is often difficult to incorporate synecological factors (e.g., competition) or life-history characteristics and habitat affinities of individual species in models (McDonald and Brown 1992).

Brown (1971, 1978) first analyzed Great Basin mountaintop faunas and concluded that previously continuous populations have been undergoing slow but continuous extirpations without concomitant colonizations because intervening inhospitable lowland habitats were believed to limit dispersal between ranges. Brown's (1971) initial analysis suggested an increase in montane mammal species richness as island (mountaintop) area increased, but subsequent discoveries of additional species occurrences and reanalyses have suggested a decreasingly important role of area (Brown 1978; Cutler 1991; Grayson and Livingston 1993; Lawlor 1998).

Most recently, Lawlor (1998) found that distributions of most species of mammals with respect to mountaintop isolation and area do not differ from random distributions and suggested that pikas (*Ochotona princeps*) exhibited one of the least nonrandom

distributions (Lawlor 1998). Lawlor (1998: 1128) concluded that most species of the current Great Basin montane fauna are "extinction-resistant woodland species capable of considerable movement among mountain ranges," this result being consistent with paleontological evidence of recent (1,000–4,000 years ago) cross-valley dispersal by the woodrat (*Neotoma cinerea*; Grayson and Madsen 2000). Thus, results of Grayson and Madsen (2000) and Lawlor (1998) have challenged, at least for some species, Brown's (1978) assumption of no recent colonizations by montane mammals of the Basin. However, Great Basin populations of *O. princeps* have frequently been treated as being fully isolated at present (Grayson and Livingston 1993; Hafner 1994; Smith 1974a).

North American pikas (*O. princeps* and *O. collaris*) likely evolved from one or more Asian species of pikas that immigrated across the Bering Strait (Dawson 1967; Kurtén and Anderson 1980). Fossil evidence suggests that ochotonid lineages have persisted in North America for at least 500,000 years (Mead 1987). *Ochotona* reached its maximum distribution during the Wisconsin glaciation (Grayson 1987; Mead 1987). Subsequent warming during the mid-Holocene forced pikas to retreat to higher latitudes and elevations (Grayson 1987; Hafner 1993, 1994). This retreat set the stage for the current relict, disjunct distribution of pikas in the Intermountain West.

Pikas provide a model system for investigating recent faunal change in montane mammal species for several reasons. Pikas are diurnal and relatively easy to detect (Smith 1974a). When used collectively, sightings, species-specific calls, and presence of fresh haypiles or feces provide a high probability of detecting the species in a single visit (Hall 1946). Thus, the problem of possibly undetected populations of montane mammals mentioned by Grayson and Livingston (1993), Lawlor (1998), and McDonald and Brown (1992) is reduced

with pikas. In addition, life history, habitat specificity, and behavior of pikas lend themselves to testing several alternative hypotheses regarding extinction dynamics (Hafner and Sullivan 1995; Smith and Weston 1990). Because of their obligate association with discontinuously distributed talus habitat, vulnerability to warmer temperatures, and tendency towards philopatry, pikas may act as early sentinels of changes in other montane mammal species. As an example, it has been predicted that of 13 species of montane mammals, only 3 would be lost from more mountain ranges than pikas would be if there were a rise of 3°C in global temperature (McDonald and Brown 1992). Compared with other montane mammal species, many aspects of pika biology have received extensive study (Smith and Weston 1990). With knowledge of pikas' paleontological history, behavior, ecology, and dispersal, reproductive, and thermal biologies, alternative hypotheses can thus be assessed with greater confidence and sophistication.

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Using the model of faunal flux occurring over tens to hundreds of millennia as a backdrop, we sought to determine if Great Basin populations reported in the 20th century (Appendix I) have suffered extirpations over decadal timescales. If extirpations had apparently occurred, we investigated biogeography (isolation and area), thermal biology, and current anthropogenic effects simultaneously as possible causes of faunal change across all populations.

We used persistence data to test 7 hypotheses (2 biogeographic, 2 climatic, and 3 human influence). The minimum-area (1st) hypothesis (Lomolino 1986) assumes that populations track a biogeographic model driven by extinction events and predicts that only populations of Great Basin pikas existing in areas having more talus than some minimum threshold should persist. The maximum-isolation (2nd) hypothesis (Lomolino 1986) assumes that populations may be modelled by an incidence function driven by colonization events and

predicts that populations closest to other colonizing sources (either the Sierra Nevada or Rocky Mountain "mainland" or nearest-neighbor populations) will be most likely to persist, other factors being equal. A 3rd hypothesis predicts that populations at hotter, drier sites should have lower probabilities of persistence if thermal biology of pikas dictates persistence of Great Basin populations. Similarly, a 4th hypothesis suggests that sites in ranges with the highest-elevation talus should have highest pika persistence if pikas are being forced to move up-slope.

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If humans have influenced pika populations recently through recreational shooting or related disturbances, then probability of persistence should increase as distance from the nearest road increases. This human-disturbance (5th) hypothesis assumes that roads (especially primary roads) provide the easiest access to taluses with pikas, potentially facilitating disturbance at these sites. If feral or native herbivory adversely affects pikas, then populations in grazed areas will be more likely to become extirpated than are populations in ungrazed areas—our 6th, ungulate grazing, hypothesis. Finally, we compared persistence of pika populations among current management jurisdictions. Assuming that more restrictive management permits fewer activities possibly detrimental to pika populations, we tested our 7th hypothesis, persistence was higher in wilderness areas than in nonwilderness Forest Service and Bureau of Land Management lands.

MATERIALS AND METHODS

Study area and field work.—We adopted for our field sampling the hydrographic definition of the Great Basin (Grayson 1993) because it has the most clearly distinguishable boundary. We excluded data on sites in the Carson Range and Wasatch Front (e.g., from Durrant 1952) because of their connection to the Sierra Nevada and Rocky mountains. Although this definition creates a domain different from that of previous biogeographic studies of Great Basin mammals, it was suitable for our purposes because we were

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TABLE 1.—Mountain ranges in the Great Basin of North America from which pikas had not been previously reported and in which pikas were not detected in additional surveys. Letters in parentheses refer to identifications of ranges in Fig. 1. Range area denotes area above 2,286 m elevation.

Mountain range	Elevation (m)		Latitude (°N)	Range area (km ²)
	Minimum	Maximum		
Clan Alpine Mountains (A)	1,166	3,038	39.4–39.9	1,149
Dogskin Mountain (B)	1,522	2,289	39.8–39.9	79
Diamond Mountains (C)	1,766	3,235	39.5–40.1	760
Humboldt Range (D)	1,265	2,997	40.2–40.7	697
Jarbridge Mountains (E)	1,823	3,289	41.7–41.9	126
Seven Troughs Range (F)	1,278	2,373	40.3–40.7	335
Snake Range (G)	1,610	3,981	38.7–39.6	2,109
Sonoma Range (H)	1,330	2,864	40.5–41.0	643
Spring Mountains (I)	853	3,633	35.6–36.5	2,168

interested in comprehensively investigating persistence of isolated populations in a relatively arid region. We obtained historical records of Great Basin pika populations from a variety of sources (Appendix I). Although dispersal within and among adjacent talus fields undoubtedly occurs to some degree within all extant populations, dispersal capability of pikas is believed to be limited to distances less than most distances between our study populations (Grayson and Livingston 1993; Hafner and Sullivan 1995; Lawlor 1998; Peacock 1997; Smith 1974a). Therefore, exchange of individuals between sites (even between adjacent ranges) is not likely to have occurred during the 10- to 100-year period we analyzed, and we thus considered each site (which we sometimes refer to as a “population”) to be an independent replicate (Appendices I and II).

We visited sites during each summer (May–August) from 1994 to 1999. During 1996 we visited all but 1 of Hall’s (1946) pika sites to minimize effects of interannual variation. In an effort to augment sample size, we also searched 9 ranges from which pikas had not been reported previously but which had occupiable talus habitat (rock diameter 0.2–1.0 m) at elevations comparable to those of Hall’s sites (Table 1).

We searched at each site for 8 h within and around talus habitat and recorded locations of pika individuals and talus patches without pikas by use of a handheld Global Positioning System instrument. Area of talus searched was based on density and arrangement of talus in the mountain range (Beever 1999). Within each talus area, we walked parallel contour transects approximately 15 m apart until the entire talus area was can-

vassed. Exhaustive searches of talus within 3.25 km of historic locations were conducted except at 5 areas with vast amounts of appropriate talus habitat (0.2–1.0 m rock diameter—Tyser 1980) nearby, at which we sampled similar nearby patches of habitat.

We recorded the presence of calling individuals, active haypiles, and individuals sighted to provide evidence for the presence of pikas at a site. Presence of fresh fecal pellets helped lead us to other types of evidence. Adoption of standardized methods such as that described above facilitates coarse-scale comparison of many sites across a broad geographical area. We also tallied the number of defecations within 1 m of the path we walked as we moved within and between talus areas (Appendix II). We classified each fecal pile as being produced either by cattle, native ungulates (pronghorn antelope, elk, mule deer, or bighorn or domestic sheep), or horses (feral and domestic).

Extirpation or absence of a mobile animal from an area is difficult to demonstrate unequivocally (Diamond 1987) and should be asserted with great caution. We thus urge the reader to consider our failures to detect populations as apparent extirpations. Because pikas may become more crepuscular and difficult to detect when weather is hotter and drier and when a site constitutes more marginal habitat, we used several techniques to increase our confidence that failures to detect pikas reflected extirpation events. To increase chance of detection, we visited populations believed to be extirpated on 2 separate occasions and consulted other researchers who had recently censused Great Basin pikas. To ensure that pikas had not evaded detection by mov-

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TABLE 2.—Results of univariate regressions on persistence (logistic regression) of Great Basin pikas. To avoid multicollinearity, only variables indicated were entered into AIC analyses, as described in Table 3. Results for variables followed by parentheses compare values of the level of the variable in parentheses against values from all other sites. Chi-square values and their associated *P*-values are Wald chi-square tests on the coefficients, and test the hypothesis that the log odds ratio for the independent variable (“Factor”) is 0.

Factor	Model coefficient	χ^2	Probability	Log likelihood test χ^2	Probability
Habitat in range ^a (large) [Habitat]	28.410	0.00	0.97	19.10	<0.0001
Maximum elevation, local talus ^a [Elevation]	0.006	4.75	0.03	16.24	<0.0001
Nearest-neighbor (not in same range) isolation	0.261	3.30	0.07	13.71	0.0002
Habitat in range (medium)	16.150	0.00	0.98	11.92	0.0006
Pika-equivalent elevation	0.009	7.02	0.008	10.84	0.001
Minimum elevation	0.001	6.88	0.009	10.12	0.0015
Longitude	-1.207	5.40	0.02	10.07	0.0015
Distance to nearest primary road ^a [RoadDist]	0.712	4.60	0.03	8.16	0.004
Latitude	-0.936	5.25	0.02	7.81	0.005
Grazing status ^a [GrazStatus]	-13.850	0.00	0.97	6.61	0.01
Management jurisdiction (wilderness)	2.996	4.85	0.03	6.26	0.012
Maximum daily temperature, August ^a (PRISM data) [MaxTemp]	-0.005	3.34	0.07	4.63	0.031
Habitat in immediate area (large)	2.300	3.93	0.048	4.46	0.035
Habitat in immediate area (medium)	2.485	3.22	0.07	3.94	0.047
Habitat in range (small)	14.200	0.00	0.98	2.97	0.085
Distance to nearest road	0.476	1.77	0.18	2.84	0.09
Management jurisdiction (United States Forest Services)	1.792	2.27	0.13	2.49	0.11
Mainland distance	-0.008	1.74	0.19	2.06	0.15
Annual precipitation (PRISM data)	0.000	1.10	0.29	1.22	0.27
Total ungulate scat	0.002	0.26	0.61	0.29	0.59
Distance to nearest population	0.012	0.21	0.65	0.23	0.63
Cattle defecations	0.001	0.60	0.81	0.06	0.80

^a Variable entered into models compared with AIC_c values; abbreviations in brackets appear in Table 3.

ing up-slope since the time of the original historic record, we searched in potential habitat all the way to the summit and used the summit as a vantage point to locate (with binoculars) other talus areas to search. Additionally, because pikas vary their daily activity patterns depending on climate and weather (Smith 1974a; Verts and Carraway 1998), we sampled within 1 h of dawn or dusk (usually both) for populations in hotter areas, including all locations of apparent extirpations. Pikas rely on vocalizations for conspecific attraction (Stamps 1988) and other purposes, especially when the talus is disturbed (references in Smith and Weston 1990; Verts and Carraway 1998). Thus, careful searches for several hours on taluses at locations of apparent extirpations should have produced at least some evidence (i.e., sighting, call, fresh haypile, or fresh feces) of an extant population. Nonetheless, despite our precautions, some unknown but

likely small proportion of the populations may have been incorrectly categorized as extant or extirpated.

Analytical techniques.—We tested competing hypotheses with univariate and information-theoretic analyses, employing dummy variables for all categorical variables. To provide a descriptive summary here, we compared selected site parameters of extant and apparently extirpated populations using 1-way analysis of variance (ANOVA). We performed univariate logistic regressions on each predictor variable against persistence and assessed significance of factors (Table 2) with likelihood ratio tests (Sokal and Rohlf 1995). Variables exhibiting possibly meaningful relationships ($P < 0.15$ —Hosmer and Lemeshow 1989) to persistence in univariate tests were entered into information-theoretic analyses that involved Akaike’s information criterion (AIC—Burnham and Anderson 1998). We

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used a less stringent critical value of alpha to ensure that potentially important interactions were not overlooked.

We divided variables with $P < 0.15$ into biogeographic, climatic, and anthropogenic categories and used a correlation matrix to identify instances of strongly multicollinear ($r > 0.7$) variables (both within each category and for the final model). We entered only the best univariate predictor of persistence from each pair of correlated variables in AIC analyses. The AIC model-selection technique determines the most parsimonious model to describe biological phenomena and can be especially useful to compare models of varying complexity (i.e., numbers of variables). Values of AIC_c , a derivative of AIC that accounts for small sample sizes (our $n = 25$ sites), were used to compare strength of competing models.

Biogeographic effects.—Biogeographic perspectives on montane mammals of the Great Basin have followed the traditional island biogeography model, viewing mountaintops as islands isolated from mainland populations in the Sierra Nevada or Rocky Mountains by a sea of inhospitable low-elevation valleys. To test for biogeographic effects, we first used data on isolation-from-mainland distances of areas above 2,300 m (7,500 ft) from Lawlor (1998). For populations not included in Lawlor's (1998) work, we defined distance from mainland as the measured distance between the study site and the 2,286-m contour of either the Sierra Nevada or Rocky Mountains (based on affinities indicated by Hafner and Sullivan's (1995) genetic analyses) on a 1:3,168,000 scale United States Geological Survey base map. We additionally used geographic information systems to measure isolation of pikas from the absolute closest population and the nearest population not in the same mountain range ("nearest-neighbor" distance).

Because talus habitable by pikas occupies different proportions of different ranges, we also analyzed persistence using categorizations of talus area at local (within 0.8-km radius) and mountain-range scales (Beever 1999). From previous literature, these spatial scales are known to correspond to dispersal distances commonly reported within a season and over longer time-scales (Hafner 1994; Hafner and Sullivan 1995; Peacock 1997; Smith 1974a; Smith and Weston 1990).

Climate change and pika thermal biology.—

To examine possible population losses related to climate change and pika thermal biology, we examined relationship of persistence to several values: minimum elevation at which pikas were observed or reported; elevation midpoint of the reported population; and "pika-equivalent elevation" (Hafner 1993), a variable represented by the equation

$$E (m) = 14,087 - 56.6 (^\circ N) - 82.9 (^\circ W).$$

In the equation, E is the minimum elevation (in m) of *O. princeps* populations throughout North America, and $^\circ N$ and $^\circ W$ are the latitudinal and longitudinal positions (in decimal degrees) of the site. We also recorded maximum elevation of talus within a 3-km radius of each site and within the mountain range (or within 5 km for sites not in ranges) to test whether ability to migrate up-slope affected persistence. To more directly assess climatic influence, for each site we obtained parameter-elevation regressions on independent slopes model (PRISM)-modeled values of annual precipitation and means of daily maximum temperature for June, July, and August, averaged across 1961–1990 at a 4-km resolution (PRISM—Daly et al. 1994). Here we report only the best predictor of persistence from among these PRISM variables.

Anthropogenic and ungulate effects.—We mapped study sites onto 1:100,000-scale maps of management jurisdiction. Jurisdictional status of pika sites (Appendix II) reflects the federal resource agency currently responsible for managing the area where populations occurred. Wilderness sites had resource conservation as a primary management objective and included 5 wilderness areas administered by the United States Forest Service, 1 wildlife refuge (sites 21 and 22), and 1 wilderness study area administered by the Bureau of Land Management (site 20). To examine more direct anthropogenic effects on persistence of populations, we measured distance of each location with a historical population to the nearest road and to the nearest primary road (Appendix II). We defined roads as any travel-way other than a trail that appeared on 1:100,000-scale topographic maps and primary roads as roads that can be traveled in summer without a 4-wheel-drive vehicle. Primary roads appear distinct from more primitive road types on topographic maps, and we verified the distance between each site and nearest primary

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road during our travel to and in the vicinity of sites.

To gauge effects of introduced and native grazers, we characterized each site as grazed or ungrazed (Appendix II) based on management mandates and on conversations with local resource personnel knowledgeable of the long-term grazing histories at our sampling areas. Grazed sites reflected instances in which significant (i.e., more than occasional or trespass) grazing by cattle, native ungulates, or horses occurred at or near taluses for more than half the period since the historic pika record. We assumed that fecal tallies roughly approximated the relative intensity of recent use by each group near talus areas, and we used these tallies to confirm characterizations of grazing status. Because response to disturbance in alpine and subalpine areas depends critically on severity of disturbance (Chambers 1997), we regressed persistence on counts of defecations of cattle, horses, other ungulates, and all ungulates combined.

RESULTS

Patterns of persistence and extirpation.—We could not detect pikas at 6 of 25 resampled populations (Fig. 1). At 1 additional site that was comprehensively searched (Cougar Peak; Appendix II), we could detect only 1 individual. Thus, we classified that population as functionally extirpated. This assumption of functional extirpation was corroborated with a resurvey of the Fort Bidwell site, at which we detected 1 individual in 1996 but none in 1999.

The 7 apparent extirpations occurred primarily in livestock-grazed areas (7 of 7 instances); at sites not in mountain ranges or in ranges with small amounts of talus habitat (6 of 7); in areas having small amounts of talus habitat within 0.8 km (4 of 7); and on lands administered by the Bureau of Land Management (4 of 7 instances; Appendix II). Six of the 7 apparent extirpations, including all 3 recorded locations of *O. p. schisticeps* from Nevada, occurred in the northwestern corner of the Great Basin. Apparently extirpated populations were located at lower absolute (ANOVA; $F =$

14.5; $d.f. = 1, 23$; $P = 0.0009$) and pika-equivalent elevations (ANOVA; $F = 15.7$; $d.f. = 1, 23$; $P = 0.0006$) and nearer to primary roads (ANOVA; $F = 8.1$; $d.f. = 1, 23$; $P = 0.009$) than were extant populations. The 9 additional ranges with high-elevation talus we surveyed (Table 1) did not contain pikas, although searches were not comprehensive in the Jarbidge, Spring, or Snake ranges. Pikas have not been found in an additional 27 other Great Basin ranges investigated by other researchers (C. Ray, in litt.).

Biogeographic and climatic hypotheses.—Extinction patterns in Great Basin pika populations were consistent with predictions of the minimum-area (1st) hypothesis but not with predictions of either a maximum-isolation or compensatory pattern (Fig. 2a; see Lawlor 1998:1119 for graphical predictions for each hypothesis). In contrast to populations not in ranges or in ranges with little habitat, populations in ranges having moderate or large amounts of talus usually remained extant (17 of 18 instances). Amount of talus habitat in the range was the strongest univariate predictor of population persistence (Table 2). This factor also appeared in the most parsimonious AIC-selected model (Table 3). Distance to mainland (Rocky Mountain or Sierra Nevada) or absolute nearest colonizing sources did not significantly predict persistence ($P > 0.15$; Table 2). Nearest-neighbor distance strongly predicted persistence but in a manner contrary to expectations: extirpated sites had closer nearest-neighbors than did extant populations ($\bar{X} = 19.9$ versus 42.5 km). We assumed this result to be spurious, and did not enter the variable into information-theoretic analyses.

Extirpated populations were located at significantly lower minimum-encounter and pika-equivalent elevations. Five of the 7 sites with apparent extirpations had among the most negative residuals of elevation when regressed against latitude (Fig. 2b). Extant sites received 19.6% less annual precipitation (ANOVA, $P = 0.30$) and aver-

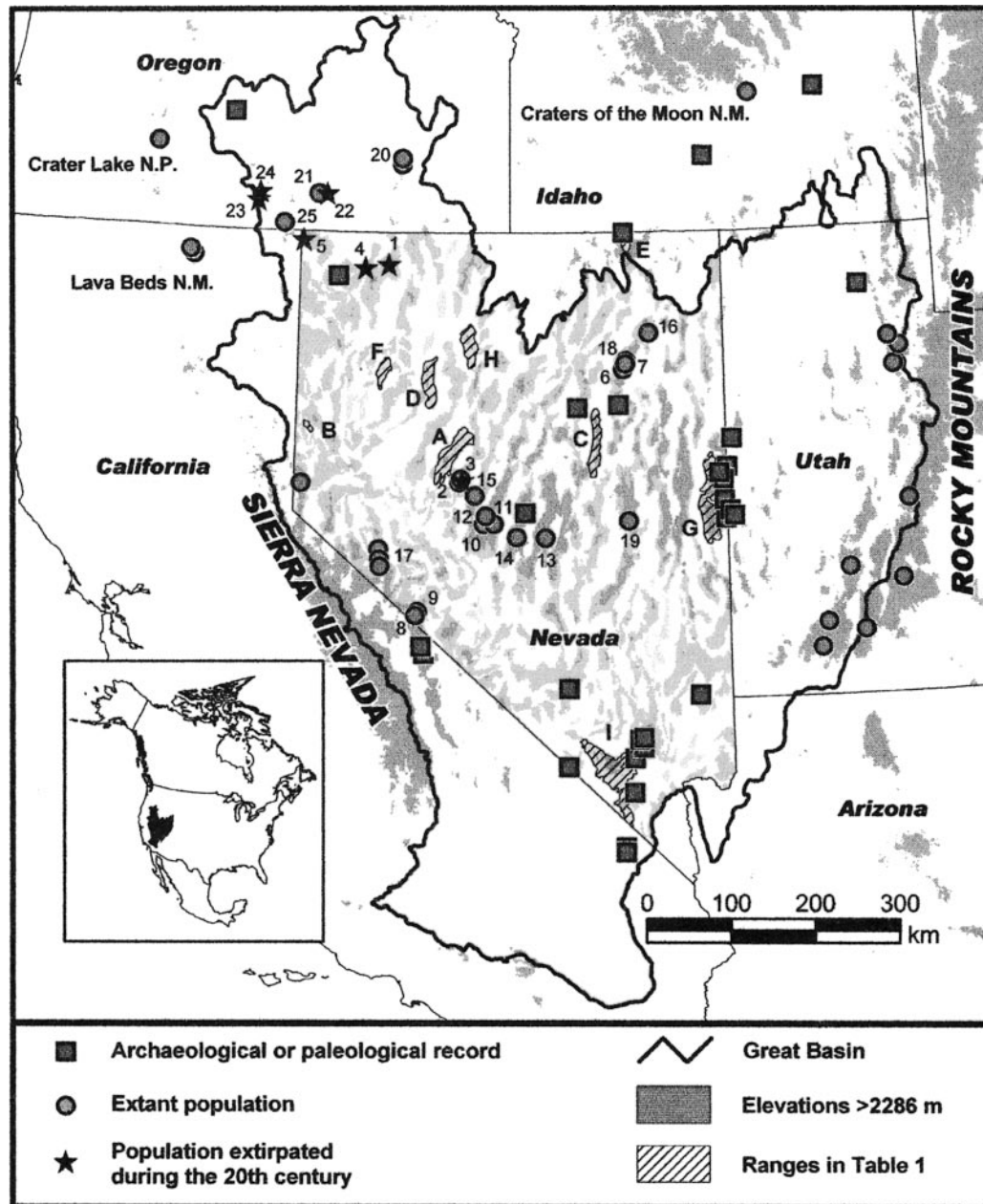


FIG. 1.—Locations of archaeological and contemporary records of pikas (*Ochotona princeps*) and populations presumed to be extirpated in the Great Basin–Mojave Desert region (as defined in Brusard et al. 1998), United States. Although the region boundary differs slightly from the hydrographic Great Basin in the far southwestern and southeastern corners, no sampling locations occurred in or near areas of discrepancy. Lettered mountain ranges possessed talus habitat at high elevations, but we found no pikas there during exploratory searches (also see Table 1). Lighter shading denotes mountain ranges defined by McLane (1978). Numbers refer to site number in Appendix I. Extant locations in Utah were reproduced from Durrant (1952). These sites were not sampled in this study (see text) but are presented for greater completeness. Sites on the eastern slope of the Sierra Nevada Mountains were too numerous to include with clarity.

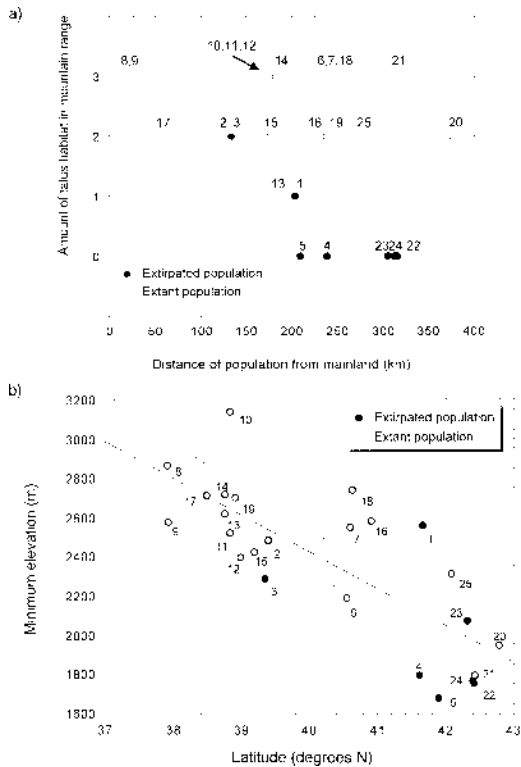


FIG. 2.—a) Relationship between degree of isolation from mainland (i.e., Sierra Nevada or Rocky Mountains) and categorical estimation of talus habitat within the mountain range for extant (open circles) and apparently extirpated populations (closed circles) of pikas (*Ochotona princeps*). Numbers refer to site numbers in Appendix I. b) Relationship between minimum elevation at which pikas were encountered or (if extirpated) reported and latitude for extant (open circles) and apparently extirpated populations (closed circles) of *O. princeps* in the Great Basin. Regression is described by the equation Minimum elevation (m) = 9943.3 - 188 (latitude, °); $r^2 = 0.61$. Dashed lines denote 95% confidence interval for the linear regression, and numbers near selected locations refer to site numbers in Appendix I.

aged daily maximum temperatures 7.7–10.2% higher than those of extant sites during June, July, and August ($P = 0.04$ to 0.08), consistent with predictions of the 3rd hypothesis. Maximum elevation of talus near sites (4th hypothesis) predicted pika persistence better than any other climate-

related variable did (Table 2) and, among models we compared, appeared in all of the 9 models with the greatest strength of evidence in support of them (Table 3).

Human-influence hypotheses.—Greater distances from the nearest road (of any type) correlated with persistence ($P = 0.09$; Table 2). Increasing distance to the nearest primary road exhibited even stronger correlation with persistence, significantly ($P = 0.004$; Table 2) increasing probability of persistence and appearing as 1 of 3 factors in the best model in information-theoretic analyses (Table 3), consistent with predictions of the 5th hypothesis. Although extirpated populations were significantly closer to primary roads ($\bar{X} = 1.75$ versus 4.63 km; $P = 0.009$) than were extant populations, we detected abundant evidence of direct human influence at only 3 of 7 sites no longer supporting pikas. At 1 site, about half of the talus area was excavated and used as a “borrow pit” for road maintenance. At another site, the talus area apparently was used extensively as a dump site. Carvings in aspen tree trunks suggested extensive human use of Smith Creek since at least the 1930s, and we found numerous gun shells on taluses there.

Results of the effects of presence and intensity of grazing on pika populations (6th hypothesis) were mixed. Grazing status showed a significant ($P = 0.01$) negative correlation with persistence (Table 2), as all 7 extirpations occurred in livestock-grazed areas ($n = 14$ sites), compared with 1 extirpation out of 11 ungrazed sites. Furthermore, the highest-ranking model that included grazing status in AIC analyses, which was 3rd-highest overall, had $\Delta < 2$ (Table 3), suggesting that the model has “substantial evidence” to support it (Burnham and Anderson 2001:114). However, the highest-ranking model had 2.4 times as much support as did this model (Table 3). Absence of the grazing-status variable in the 2 highest-ranking models may have occurred in part because ungrazed sites were located at higher minimum elevations ($P <$

TABLE 3.—Comparison of ability of various models to predict probability of population extirpation, ranked in order of increasing AIC_c values (Akaike's information criterion, adjusted for small sample size). Abbreviations of model variables refer to variables with “#” in Table 2. “Model” contains the variables included in each model, maximum log-likelihood ($\log L$) refers to the value of the maximized log-likelihood over unknown parameters (given the data and model), k is number of estimated parameters in the model, AIC_c is value of AIC corrected for small sample sizes, Delta is difference of AIC_c for a particular model from the best model, and Weight is a factor that reflects how good a model is relative to the rest.

Model	Log-likelihood (-2)($\log L$)	k	AIC_c	Delta	Weight
Elevation Habitat RoadDist	4.852	4	14.852	0.000	0.2627
Elevation Habitat	8.414	3	15.557	0.705	0.1847
Elevation RoadDist GrazStatus	6.625	4	16.625	1.773	0.1083
Elevation RoadDist	10.300	3	17.443	2.591	0.0719
Elevation Habitat RoadDist GrazStatus	4.701	5	17.859	3.007	0.0584
Elevation	13.408	2	17.953	3.101	0.0557
Elevation GrazStatus	10.892	3	18.035	3.183	0.0535
Elevation Habitat MaxTemp	8.204	4	18.204	3.352	0.0492
Elevation Habitat GrazStatus	8.410	4	18.410	3.558	0.0444
Habitat RoadDist	11.482	3	18.624	3.773	0.0398
Elevation MaxTemp	12.353	3	19.496	4.644	0.0258
Elevation RoadDist MaxTemp	9.870	4	19.870	5.018	0.0214
Elevation GrazStatus MaxTemp	10.306	4	20.306	5.454	0.0172
Habitat MaxTemp	17.297	3	24.440	9.588	0.0022
Habitat	20.728	2	25.273	10.421	0.0014

0.05) and tended to have larger amounts of nearby habitat (Appendix I). Neither total number of ungulate defecations nor cattle defecations alone at sites predicted population persistence (Table 2). Neither the number of horse defecations nor those of other ungulate defecations showed any relation to persistence of pikas.

Lands administered by the Bureau of Land Management experienced more population extirpations (4 of 6) than did lands administered by the United States Forest Service (2 of 8 populations) or wilderness areas (1 of 11 populations; Appendix II), consistent with predictions of the 7th hypothesis.

DISCUSSION

This is 1 of few documented instances in which a medium- to small-sized mammal in North America has apparently experienced extirpations at a bioregional scale over the span of only a few decades (55–86 years since last record—Appendix I). In contrast

to previous analyses of montane mammals, this analysis provides a step toward merging explanations for persistence that span temporally from human generation times to ecological scales to evolutionary time-scales. As such, we were able to investigate the interaction of natural stochasticity present in a rare, discontinuously distributed organism with external climatic and human-mediated influences.

Because it was not obvious to us a priori which combination of biogeographic, climatic, and anthropogenic variables would best explain metapopulation dynamics across the Great Basin, we used univariate regressions as a filter to select variables to enter into AIC analyses. Our naturally limited sample size was insufficient to address even a truncated set of combinations of all potentially meaningful variables. However, Burnham and Anderson (2001) recommend that biological, rather than statistical, considerations drive selection of the combinations of variables to include in models to

be compared with information-theoretic methods. Consequently, we caution that our approaches should be considered exploratory, and they do not provide cause-and-effect or confirmatory evidence about factors that may explain the apparent extirpations.

Biogeographic hypotheses.—Because of their obligate association with discontinuously distributed talus habitat, pikas exhibit greater isolation than does perhaps any other montane mammal in the Great Basin and are isolated at both within-range and between-range scales. Our finding of no relationship between isolation from mainland or nearest neighbors and persistence, predicted by the 2nd hypothesis, suggests that contemporary populations of Great Basin pikas are not a colonization-driven system, a result consistent with previous work (e.g., Lawlor 1998) and other lines of evidence. Pikas are highly philopatric, and only 25% of all juveniles may attempt dispersal (Smith 1987). Additionally, the likelihood of successful dispersal across nontalus habitat may be low for pikas (Smith 1974a, 1974b, 1980). Maximum dispersal distances are typically 3 km (Smith 1974b), with the vast majority consisting of much shorter distances. Hafner (1994) estimated that very few colonizations across distances of >20 km have occurred over the last 6,000 years in the southern Rocky Mountains. Given these observations, natural recolonization of extirpated localities in the Great Basin (assuming they are still suitable for pikas) under current climatic conditions seems improbable.

Longer dispersal events may be possible, however, in more mesic, higher-elevation habitats such as the Sierra Nevada Mountains of California (one 2-km dispersal observed per year—Peacock 1997) or the Rocky Mountains (Hafner 1994). Using comparisons of genetic similarity, Hafner and Sullivan (1995) found that pika metapopulations are separated by 10–100 km and postulated that maximum dispersal distance for an individual pika would probably be 10–20 km. The degree to which these

distances are traversed currently by pikas in the Great Basin could be assessed most precisely by use of combined mark–resight and genetic techniques (Peacock 1997).

Amount of talus habitat at the mountain-range scale was the strongest univariate predictor of persistence. Additionally, amount of talus habitat occurred in the best model for persistence using AIC model selection, lending further support to the 1st hypothesis. The importance of habitat area has also been demonstrated at smaller spatial scales by Smith (1980), who found that all cases of population extinctions occurred on small or medium-sized patches at Bodie in the Sierra Nevada of California. The vast difference in spatial scale complicates comparisons between Smith's (1980) investigations and ours, however. For example, different mechanisms or combinations of factors may operate at different scales to produce the similar pattern of higher rates of disappearance in smaller patches. Whereas habitat area may influence species richness of birds or mammals by sustaining greater habitat diversity (Brown 1978; Johnson 1975), obligate association of pikas with talus precludes the importance of coarse-scale habitat diversity for pika persistence. More likely, persisting in ranges with minimal habitat or at locations not in ranges is difficult because potential rescue effects (Brown and Kodric-Brown 1977) are unlikely. Furthermore, in those cases populations are limited to small sizes, which increases their vulnerability to stochastic events (Caughley 1994; Newmark 1995).

Because talus area remains constant over ecological timescales, space seems an unlikely direct determinant of extinction over the short timescales we investigated, except to the extent that it forces pikas into a small-population dynamic (Caughley 1994). This latter possibility, of synergistic influence with other threats, could well be magnified if increasing temperatures reduce the effective area of habitable talus in an area. Occurrence of extirpations without detectable change in (talus) habitat abun-

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dance, quality, or spatial pattern highlights the importance of including a broad range of variables in and field-truthing habitat-based models of trend for vertebrate populations.

Because previous biogeographic investigations have included only a subset of the available Great Basin records for any particular species, they provide an incomplete (and perhaps biased) picture of how species respond to factors driving persistence or extinction within a region. These studies admittedly had goals very different from those of this study, though, and have in fact contributed to a better understanding of trends in montane faunas.

Climatic hypotheses.—Although there has been increasing awareness of long-term trends in climatic variables (e.g., changes in global temperature), effects on vertebrates are just beginning to be understood. Our finding that maximum elevation of talus habitat occurred in all of the 9 highest-ranking (yet in none of the 8 lowest-ranking) models for persistence in information-theoretic analyses (lending support to the 4th hypothesis) suggests that thermal effects have influenced recent persistence trajectories of Great Basin populations of pikas. Thus, warmer temperatures seem likely to be contributing to apparent losses that have occurred at a pace significantly more rapid than that suggested by paleontological records. Maximum elevation of talus at local and mountain-range scales relates to climatic influence because it denotes how far up-slope pikas can migrate in relatively contiguous taluses under increased temperatures. Importance of thermal biology is supported more forcefully by the fact that extirpations occurred in 3 low-elevation areas in close proximity to high-elevation populations that remained extant (i.e., at sites within the Desatoya, Hart, and Ruby mountains). In the latter instance, we searched Thomas Canyon around elevations at which pikas were collected in summer 1956 and detected abundant pikas at 2,743 and 2,895 m elevation but none at 2,375 m.

Climatically induced thermal stress on Great Basin pikas could influence their distributions in several ways. Rapidly increasing temperatures could change the composition or relative abundance of plants in and around talus areas to a mix with which pikas have not coevolved. Quantitative vegetation data collected over decades would be necessary to address this possibility rigorously. Alternatively, higher summer temperatures could permit less midday foraging time (Smith 1974a), perhaps preventing pikas from gaining sufficient body mass and collecting sufficient hay to overwinter successfully. Compared with other montane mammals, energetic demands are exacerbated for pikas, in part because they are active year round. Thus, pikas make up to 13 haying trips per hour to create average-sized haypiles (Dearing 1997) and need to fill their stomach 9 times daily (Smith and Weston 1990). Alternatively, rises in summer temperature may modify the thermal climate of talus to the point that the relatively low upper lethal temperature (Smith 1974a) or capacity of pikas to thermoregulate behaviorally is exceeded. This seems especially likely in structurally simple (i.e., small-diameter rocks of homogeneous size) or shallow talus, where thermal refugia are less well buffered from ambient environmental conditions. The relationship between extant populations and climatic factors across the range of pikas in North America was suggested strongly by Hafner (1993), who found that species of *Ochotona* are restricted to cool, moist microhabitats within regions having short summers and freeze-free periods, long winters, and mean annual precipitation >30 cm. Increasing temperatures could cause the range of potential pika habitat in a mountain range to move up-slope (Peters and Darling 1985), altering the spatial distribution of the metapopulation by rendering unsuitable previously habitable talus patches or by fragmenting higher-elevation talus.

If extirpations of pika populations in the past few decades were driven by climatic

?13

?14

changes, then rapid climatic alteration simply accelerated (greatly) the rate of population loss observed through paleontological evidence in the Holocene and Pleistocene periods (Grayson 1987, 1993). Previously extirpated populations, considered "extralimital" to current distributions, occurred at elevations between 730 and 2,070 m and were extant 7,200–34,000 years ago (Grayson 1987, 1993). Latitudinal gradients in pika distribution and persistence, presumably tied to gradients in climate, have existed at least since the onset of the Holocene (Grayson 1993; Grayson and Livingston 1993). Similarly, because northern populations presumably have been separated from the mainland for shorter time periods, northern and southern populations may not exhibit comparable extinction rates (Grayson and Livingston 1993). If this were the case, the direct prediction would be that southern populations, separated for a longer time period, will exhibit greater population losses. However, we found the opposite: probability of persistence decreased significantly ($P = 0.005$) with increasing latitude (Table 2). An alternative interpretation of this result is that marginal southern populations were extirpated long ago, but northern populations are still on the steeper part of the exponential curve of extinction rate over time. This interpretation supports a relict climatic effect on population persistence and suggests that northern populations had a greater extinction debt (Tilman et al. 1994).

Human-influence hypotheses.—Although biogeographic analyses generally have considered Great Basin mountaintops to be oases of low anthropogenic influence because of their isolation, at least 12% of tundra ecosystems in the western United States had experienced some level of historic-era human-induced disturbance by 1978 (Brown et al. 1978). The short growing season, variable precipitation, relatively low primary productivity, temperature fluctuations, high wind speeds, and shallow, weakly developed soils of alpine and subalpine

systems can compound effects of disturbance and make these ecosystems among the most difficult to restore (Butler 1995; Chambers 1997).

Distance of pika populations from primary roads significantly predicted population persistence in univariate analyses and was a component of the best model using AIC model-selection techniques, consistent with predictions of the 5th hypothesis. Because extirpated populations also occurred at lower elevations and at areas with less habitat, however, we cannot refute the possibility that apparent influence of proximity to roads was confounded by higher temperatures and sparser habitat at lower elevations.

All apparent population extirpations occurred in areas open to livestock grazing, consistent with predictions of the 6th hypothesis. However, grazed areas occurred at lower elevations and had less talus habitat than did ungrazed areas. These results will, we hope, stimulate further research on the relationship between domestic and feral ungulate grazing and pika populations. Because pikas exhibit behavior consistent with central-place foraging, intensity of pika foraging generally decreases, and costs associated with foraging generally increase with increasing distance from talus (Huntly et al. 1986). Furthermore, risk of predation increases as pikas must forage greater distances, and pikas can safely use broader areas when artificial talus cover is provided (Huntly et al. 1986). Therefore, cattle or horses may negatively influence pikas if the ungulates graze in areas within 20–50 m of talus. If significant interaction is occurring, it need not be through exploitative competition for food. Rather, indirect influence could occur via trampling of soils or vegetation, which occurs in both cattle (Weltz et al. 1989) and horse grazing (Beever et al., in press).

In contrast, grazing should be implicated with great caution when interpreting declines of pikas and other talus inhabitants. First, the solid nature of talus rock may pre-

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vent direct interaction between large herbivores and pikas; we observed an active haypile directly under a well-traveled horse trail in the Desatoya Mountains and several haypiles near other trails. Similarly, cattle appeared to avoid all opportunities to cross talus, especially on steep slopes. Second, grazing status of very broad areas may correspond only loosely with grazing pressure in the immediate vicinity (i.e., within 50 m) of talus areas because steep terrain or rock formations may largely prevent livestock or feral horses from accessing talus margins. Third, whereas cattle and horses primarily consume graminoids (Hanley and Hanley 1982), pikas are generalist herbivores. Fourth, it may be difficult to model diet and behavior of generalized herbivores such as the pika because of possible nutrient-balancing constraints unrelated to interspecific interactions and inter- and intraspecific variability in plant chemistry (Rapport 1980).

Although we failed to reject the hypothesis that persistence and extant population sizes should be highest at wilderness sites (7th hypothesis), this finding is confounded by greater available habitat at wilderness area sites. This confounding is not unique to our study; Norton (1999) similarly found that protected reserve areas are concentrated in the high-elevation and steep, infertile parts of landscapes. In North America, most existing national parks were established to protect scenic and geological (rather than biological) wonders, which are often located at higher elevations and have more talus-producing formations (Wagner et al. 1995).

Management influence on Great Basin pikas is difficult to assess for other reasons as well. Although Hart Mountain ($n = 2$ sites) was established as a Refuge in 1936, 7 of our 11 wilderness sites did not receive formal wilderness designation until 1989. Thus, because no surveys were performed across sites before 1989, it remains uncertain how wilderness management has affected Great Basin pikas during the 20th century. Furthermore, in the Great Basin, the Bureau of Land Management was as-

signed jurisdiction of lower-elevation lands, which were often in poorer condition than were Forest Service lands at the inception of the Bureau of Land Management in 1934.

Pikas in the Great Basin appear to have undergone significant losses (>25% of historic sites) during the last half century. The inclusion of some anthropogenic as well as natural variables in models selected using AIC methods in this exploratory analysis suggests that current anthropogenic influences (i.e., grazing status, proximity to roads) may have combined with factors acting over longer timescales (e.g., climate, habitat area) to produce fairly rapid apparent extirpations of pikas in the Great Basin. Thus, anthropogenic factors should be used to refine biogeographic and metapopulation models of species incidence because they can affect the fundamental biogeographic processes of immigration, extinction, and evolution.

However, there are caveats to this interpretation. Long-term studies are needed to verify these patterns of apparent extirpation and to more firmly establish their causes. Furthermore, to fully evaluate the relative utility of management actions for restoration or conservation of vulnerable populations in the Great Basin, we recommend manipulative experiments to partition natural variability more clearly from anthropogenic influence. Although some combination of factors investigated here may affect pika populations in other geographic regions, genetic divergence among subspecies resulting from long-term isolation demands that the domain of inference for our findings be restricted to the Great Basin.

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APPENDIX I

Characteristics of sites in the hydrographic Great Basin, United States, at which populations of pikas (*Ochotona princeps*) were reported during the 20th century. Site numbers identify populations in Figs. 1 and 2. Criteria for categories of occupiable talus follow Beever (1999), and pika-equivalent elevation follows Hafner (1993), "Mainland" refers to either the Sierra Nevada or Rocky Mountains, as described in text.

Site number	Location	Source ^a	Specimen date	Mountain range	Amount of occupiable talus:	
					In immediate area (0.8 km radius)	In mountain range
1	Duffer Peak ^c	a	1935	Pine Forest	Small	Small
2	Toby Canyon	a	1934	Desatoya	Large	Medium
3	Smiths Creek ^c	a	1934	Desatoya	Large	Medium
4	Summit Lake ^c	a	1936	Not in a range	Small	Not in a range
5	Fort Bidwell	a	1941	Not in a range	Medium	Not in a range
6	Long Creek	a	1928	Ruby	Small	Large
7	Three Lakes	a	1928	Ruby	Large	Large
8	Mustang Mountain	a	1933	White	Large	Large
9	Pinchot Creek	a	1933	White	Medium	Large
10	Arc Dome	a	1898	Toiyabe	Large	Large
11	South Twin River	a	1915	Toiyabe	Large	Large
12	Mohawk Canyon	a	1931	Toiyabe	Medium	Large
13	Greenmonster Canyon	a	1933	Monitor	Medium	Small
14	Mount Jefferson	a	1933	Toquima	Large	Large
15	Peterson Creek	a	1934	Shoshone	Medium	Medium
16	Steels Creek	a	1929	East Humboldt	Large	Medium
17	Big Indian Mountain	b	1947	Wassuk	Large	Medium
18	Thomas Creek	b	1956	Ruby	Large	Large
19	Currant Mountain	c	1990	White Pine	Medium	Medium
20	Kiger Gorge	d	1916	Steens	Medium	Medium
21	Stockade, Warner, Goat Creeks	d	1937	Hart	Large	Large
22	20 mi NE Adel ^c	d	1913	Not in a range	Small	Not in a range
23	Cougar Peak ^d	d	1925	Not in a range	Large	Not in a range
24	Thomas Creek Ranger Station ^c	d	1925	Not in a range	Small	Not in a range
25	Crane Mountain	d	1930	Warner	Large	Medium

^a Sources: a, Hall (1946); b, U.C. Berkeley Museum of Vertebrate Zoology records; c, Lawlor (1998); d, Verts and Carraway (1998).

^b The lowest elevation at which we detected pikas in surveys during 1994–1999 or (if undetected) pikas were reported.

^c Extirpated.

^d Functionally extirpated (only 1 individual detected).

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APPENDIX I.—Extended.

Mean latitude (°N)	Mean longitude (°W)	Pika- equivalent elevation (m)	Minimum elevation of encounter ^b (m)	Distance to mainland (km)
41.65	118.74	1,885.7	2,560	203.1
39.39	117.75	2,095.6	2,484	133.0
39.35	117.68	2,103.8	2,286	133.0
41.61	119.07	1,861.0	1,798	239.0
41.90	119.96	1,771.4	1,680	209.4
40.54	115.47	2,220.2	2,188	237.0
40.59	115.39	2,224.1	2,550	237.0
37.90	118.31	2,133.5	2,865	16.0
37.92	118.29	2,134.5	2,576	16.0
38.83	117.35	2,160.7	3,139	176.0
38.83	117.31	2,164.4	2,525	176.0
38.98	117.33	2,154.2	2,400	176.0
38.75	116.57	2,230.4	2,621	182.0
38.75	116.72	2,217.4	2,720	182.0
39.19	118.30	2,062.3	2,423	176.0
40.90	115.11	2,229.3	2,583	237.0
38.49	118.79	2,060.8	2,713	57.8
40.62	115.40	2,220.9	2,743	237.0
38.91	115.40	2,318.1	2,701	240.0
42.77	118.58	1,836.1	1,951	376.0
42.42	119.76	1,758.0	1,798	316.3
42.40	119.64	1,769.1	1,760	315.8
42.31	120.63	1,692.2	2,073	305.6
42.40	120.60	1,689.7	1,768	312.5
42.08	120.24	1,737.50	2,316	275.0

APPENDIX II

Data used to test human-influence hypotheses for pika populations of the Great Basin. In non-wilderness areas, "jurisdiction" refers to the land agency administering management at the area. Primary roads were roads passable in summer without a 4-wheel-drive vehicle.

Site number	Location	Defecations ^a			Management jurisdiction ^b	Grazing status ^c	Distance to nearest	
		Cattle	Other-ungulate	Horse			Road (km)	Primary road (km)
1	Duffer Peak ^d	100	8	0	BLM	G	2.75	2.75
2	Toby Canyon	81	31	429	BLM	G	1.25	6.00
3	Smiths Creek ^d	269	19	120	BLM	G	0.25	0.25
4	Summit Lake ^d	2	0	34	BLM	G	2.00	3.25
5	Fort Bidwell	60	10	1	BLM	G	0.50	0.50
6	Long Creek	53	2	10	USFS	G	5.50	6.75
7	Three Lakes	7	3	17	Wilderness	U	1.50	1.50
8	Mustang Mountain	0	18	23	USFS	U	0.50	1.25
9	Pinchot Creek	44	10	52	BLM	G	2.25	2.50
10	Arc Dome	126	81	2	Wilderness	U	7.75	7.75
11	South Twin River	2	4	79	Wilderness	U	8.25	8.25
12	Mohawk Canyon	197	34	0	USFS	G	2.75	3.25
13	Greenmonster Canyon	449	120	0	USFS	G	2.75	5.50
14	Mount Jefferson	18	113	0	Wilderness	U	5.25	5.50
15	Peterson Creek	117	70	0	USFS	G	0.75	2.75
16	Steels Creek	12	73	0	Wilderness	U	1.25	3.50
17	Big Indian Mountain	2	2	0	Wilderness	U	0.50	8.50
18	Thomas Creek	7	17	0	Wilderness	U	3.50	3.50
19	Current Mountain	48	3	0	Wilderness	U	1.75	5.25
20	Kiger Gorge	291	27	0	Wilderness	G	0.25	7.25
21	Stockade, Warner Crks.	5	29	6	Wilderness	U	0.75	1.50
22	20 miles NE of Adel ^d	9	119	0	Wilderness	U	2.00	4.50
23	Cougar Peak ^e	8	3	4	USFS	G	0.00	0.75
24	Thomas Creek R.S. ^d	46	5	0	USFS	G	0.25	0.25
25	Crane Mountain	27	9	1	USFS	G	0.00	2.75

^a Defecations reflect counts of fecal piles in standardized encounter surveys.

^b BLM = Bureau of Land Management; USFS = United States Forest Service; "Wilderness" defined in text.

^c G = grazed by domestic cattle or sheep grazing for >50% of the period between historic record of pikas and our sampling; U = ungrazed.

^d Extirpated.

^e Functionally extirpated (only 1 individual detected)