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ORIGINAL ARTICLE

A brief history of Great Basin pikas

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ABSTRACT

Aim Within the past few decades, seven of the 25 historically described populations of American pikas (*Ochotona princeps*) in the Great Basin of arid western North America appear to have become extinct. In this paper, the prehistoric record for pikas in the Great Basin is used to place these losses in deeper historical context.

Location The Great Basin, or area of internal drainage, of the western United States.

Methods The location, elevation, and age of all reported prehistoric Great Basin specimens of American pikas were extracted from the literature. Elevations of extinct pika populations were arrayed through time, and latitudes and longitudes of those populations used to determine changing distances of those populations from the nearest extant populations.

Results The average elevation of now-extinct Great Basin pika populations during the late Wisconsinan (*c.* 40,000–10,000 radiocarbon years ago) and early Holocene (*c.* 10,000–7500 years ago) was 1750 m. During the hot and dry middle Holocene (*c.* 7500–4500 years ago), the average elevation of these populations rose 435 m, to 2168 m. All prehistorically known late Holocene (*c.* 4500–200 years ago) populations in the Great Basin are from mountain ranges that currently support populations of this animal, but historic period losses have caused the average elevation of pika populations to rise an additional 152 m. The total elevational increase, from the late Wisconsinan and early Holocene to today, has been 783 m. As lower elevation pika populations were lost, their distribution increasingly came to resemble its modern form. During the late Wisconsinan, now-extinct pika populations were located an average of 170 km from the nearest extant population. By the late Holocene, this distance had declined to 30 km.

Main conclusions Prehistoric alterations in the distribution of pika population in the Great Basin were driven by climate change and attendant impacts on vegetation. Today, Great Basin pikas contend with both climate change and anthropogenic impacts and thus may be on the brink of extinction.

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Keywords
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INTRODUCTION

The recent discovery that seven of the 25 historically described populations of American pikas (*Ochotona princeps* Richardson) in the Great Basin of western North America appear to be extinct (Beever *et al.*, 2003) has added emphasis to earlier warnings that Great Basin populations of this animal are highly vulnerable (McDonald & Brown, 1992). Here, I use archaeological and palaeontological records to stress that these recent losses are part of a

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process that began thousands of years ago and I provide two simple measures of this process in action.

AMERICAN PIKAS: MODERN AND LATE PLEISTOCENE DISTRIBUTIONS

The American pika *Ochotona princeps* is a small (*c.* 120–180 g) diurnal herbivore related to rabbits and hares. Today, these animals are discontinuously distributed across mountainous areas in western North America, from the southern Sierra Nevada and Rocky Mountains to central British Columbia. Within this range, pikas are tightly restricted to talus slopes adjacent to the vegetation that provides their diet. The talus slopes in which pikas live not only provide protection from predators but can also provide refuge from warm temperatures. Even brief exposure to temperatures in excess of *c.* 27 °C can be fatal to them (Smith & Weston, 1990).

The geographic distribution that now characterizes pikas is recent. During the latest Pleistocene, a large form of *Ochotona*, perhaps the extinct *O. whartoni* (known from the western Arctic), was found as far east as Ontario, Canada as late as *c.* 9000 years ago (all ages in this paper are in radiocarbon years). A smaller form, perhaps *O. princeps*, lived in the eastern United States until sometime during the last glaciation, perhaps as late as 30,000 years ago or even later (Mead & Grady, 1996). The restriction of American pikas to rocky settings also seems recent. Analyses of pika remains from ancient woodrat (*Neotoma*) middens in western North America shows that at *c.* 12,000 years ago, pikas were living at relatively low elevations (< 2000 m) in areas devoid of talus (Mead, 1987; Mead & Spaulding, 1995; Rhode & Madsen, 1995).

The American pikas of the Great Basin (the area of internal drainage in the western United States) have received more scientific attention than those of any other area in North America. The Great Basin is characterized by north–south trending mountain ranges of often massive size and high elevation (> 3000 m), separated by substantial valleys dominated by xerophytic vegetation (Grayson, 1993). Since temperatures in these valleys routinely exceed those which pikas can tolerate, it is no surprise that they are now confined to a subset of Great Basin mountain ranges. Pikas have weak dispersal abilities (Smith, 1974a; Smith & Weston, 1990), making it highly likely that the ancestors of today's pikas colonized these and other Great Basin ranges during the Pleistocene, with their current distribution reflecting the results of differential extinction across these ranges (Brown, 1971, 1978).

The archaeological and palaeontological records for pikas in the Great Basin provides strong support for this view of Great Basin pika history, documenting their Pleistocene and Holocene presence on mountains and in valleys where they no longer exist (e.g. Grayson, 1977, 1987; Mead *et al.*, 1982; Mead, 1987). This record also suggests that prehistoric pika extinctions were driven by increasing temperatures, decreasing effective moisture and attendant changes in plant communities (Grayson, 1993; Mead & Spaulding, 1995), a conclusion that matches the known habitat requirements of these animals (Smith, 1974b; Hafner, 1993, 1994). This inference is also consistent with the demonstration by Beever *et al.* (2003) that the sites from which pikas disappeared during historic times are marked by (among other things) lower precipitation and higher temperatures than are those at which pikas have persisted.

METHODS

Prehistoric pika specimens – bones, teeth, and fecal pellets – have been retrieved from traditional archaeological and palaeontological sites and from woodrat middens within the Great Basin. The location, elevation, and age of all such specimens was extracted from the literature, providing a total of 72 chronologically and/or geographically distinct prehistoric pika populations for this region (see Table 1 and Fig. 1). Of these, 66 are from areas in which pikas no longer exist. Fifty-seven of these have been sufficiently well-dated that they can be placed in at least a general chronological framework. In all cases, specimens whose stratigraphic integrity has been questioned were eliminated from consideration. Most notably, these include the specimens from the Connley Caves, Oregon (Fig. 1, site 1) that have routinely been assigned to the early Holocene (Grayson, 1979) but which may be late Wisconsinan in age (Jenkins *et al.*, 2002; D. L. Jenkins, pers. comm.).

The means by which individual pika specimens were introduced into these sites is generally unknown. Insofar as they were introduced by raptors, the elevation of the site in which the remains were found may not match the elevation at which the pikas themselves were living. As a result, it is fortunate that many of the prehistoric records are derived from pika dung pellets from woodrat middens (Table 1). As Mead & Spaulding (1995) and Rhode & Madsen (1995) have observed, these pellets were most likely collected by woodrats and it is extremely unlikely that they were derived from elevations significantly different from the middens themselves. Since the pellet records are often from the same general areas and elevations that have provided skeletal records, there is little reason to think that the use of standard archaeological and palaeontological data has biased the results presented here. I return to this issue below.

The latitudes and longitudes of these sites were obtained in one of three ways. Most were determined using the TopoZone interactive coordinate display (http://www.topozone.com). Where this was not possible, values were taken from the published literature. In a few cases, neither sufficiently exact site locations nor latitudes and longitudes had been published and the relevant information was obtained from the investigators involved.

The locations of modern pika populations were also taken from the standard literature (Grinnell, 1918; Howell, 1924; Bole, 1938; Hall, 1946, 1951; Durrant, 1952; Verts & Carraway, 1998; Beever *et al.*, 2003). Pika records for the White Mountains, California, have been augmented by my own field work in the vicinity of the archaeological sites listed in Table 1. Distances between prehistoric populations and extant populations were

Table 1 Prehistoric Great Basin sites containing pika remains, from north to south. Sites that have provided pika dung pellets are indicated in italics; all others contain skeletal materials. Numbers in parentheses in the first column indicate the location of sites in Fig. 1

Site and excavation level (if appropriate)	Latitude	Longitude	Elevation	Distance to nearest extant population (km)	Age*	Source†
Connley Cave 4, Fort Rock Basin, OR: Stratum 3 (1)	43.15	121.00	1356	55: Paulina Lake, OR	ND	1
Connley Cave 4, Fort Rock Basin, OR: Stratum 4 (1)	43.15	121.00	1356	55: Paulina Lake, OR	ND	1
Connley Cave 5, Fort Rock Basin, OR: Stratum 3 (1)	43.15	121.00	1356	55: Paulina Lake, OR	ND	1
Deer Creek Cave, Jarbidge Mountains, NV: 84–90″ (2)	41.46	115.25	1770	115: Steels Creek, NV	EH	2
Deer Creek Cave, Jarbidge Mountains, NV: 90–96″ (2)	41.46	115.25	1770	115: Steels Creek, NV	EH	2
Deer Creek Cave, Jarbidge Mountains, NV: 108–114″ (2)	41.46	115.25	1770	115: Steels Creek, NV	LW	2
Deer Creek Cave, Jarbidge Mountains, NV: 120–126″ (2)	41.46	115.25	1770	115: Steels Creek, NV	LW	2
Deer Creek Cave, Jarbidge Mountains, NV: 126–130″ (2)	41.46	115.25	1770	115: Steels Creek, NV	LW	2
Hanging Rock Shelter, Hanging Rock Canyon, NV: Stratum 2/4 (3)	41.31	119.27	1725	65: Warren Peak, CA	ND	3
Hanging Rock Shelter, Hanging Rock Canyon, NV: Stratum 4 (3)	41.31	119.27	1725	65: Warren Peak, CA	ND	3
Hanging Rock Shelter, Hanging Rock Canyon, NV: Stratum 5 (3)	41.31	119.27	1725	65: Warren Peak, CA	EH	3
Raven Cave 1a, Raven Cave, NV (4)	40.56	114.05	1510	85: Steels Creek, NV	LW	4
Mad Chipmunk Cave, Toano Range, NV (5)	40.49	114.16	1859	70: Steels Creek, NV	ND	5
Top of the Terrace 4A, Goshute Range, NV (6)	40.36	114.20	2012	75: Steels Creek, NV	LW	4
Bronco Charlie Cave, Ruby Mountains, NV (7)	40.10	115.31	2134	40: Long Creek, NV	ND	6
Mineral Hill Cave, Sulphur Spring Range, NV (8)	40.08	116.05	2060	70: Long Creek, NV	LW	7
Serendipity Cave, Roberts Mountains, NV: Pre-Mazama (9)	39.49	116.19	2134	130: Long Creek, NV	EH	8
Granite Canyon 1, Deep Creek Range, UT (10)	39.40	113.50	2070	160: Current Mountain, NV	LW	9
Crystal Ball Cave, Snake Valley, UT (11)	39.29	114.02	1760	135: Current Mountain, NV	LW	10
Smith Creek Cave, Snake Range, NV: Grey (12)	39.21	114.05	1950	125: Current Mountain, NV	ND	11
Smith Creek Cave, Snake Range, NV: Reddish-Brown (12)	39.21	114.05	1950	125: Current Mountain, NV	LW	11
Smith Creek Cave 4, Snake Range, NV (12)	39.21	114.05	1950	125: Current Mountain, NV	LW	9
Smith Creek Cave 5, Snake Range, NV (12)	39.21	114.05	1950	125: Current Mountain, NV	LW	9
Council Hall Cave, Snake Range, NV (12)	39.20	114.06	2040	120: Current Mountain, NV	LW	11
Streamview Rockshelter 1, Snake Range, NV (12)	39.20	114.05	1860	125: Current Mountain, NV	LW	9
Streamview Rockshelter 2, Snake Range, NV (12)	39.20	114.05	1860	125: Current Mountain, NV	LW	9
Streamview Rockshelter 3, Snake Range, NV (12)	39.20	114.05	1860	125: Current Mountain, NV	MH	9
Arch Cave 2A, Snake Range, NV (12)	39.17	114.05	1980	115: Current Mountain, NV	LW	12
Gatecliff Shelter, Toquima Range, NV: Stratum 1, H3 (13)	39.00	116.47	2319	30: Mt. Jefferson, NV	LH	13
Gatecliff Shelter, Toquima Range, NV: Stratum 9 (13)	39.00	116.47	2319	30: Mt. Jefferson, NV	LH	13
Gatecliff Shelter, Toquima Range, NV: Stratum 20 (13)	39.00	116.47	2319	30: Mt. Jefferson, NV	MH	13
Gatecliff Shelter, Toquima Range, NV: Stratum 22 (13)	39.00	116.47	2319	30: Mt. Jefferson, NV	MH	13
Gatecliff Shelter, Toquima Range, NV: Strata 24–25 (13)	39.00	116.47	2319	30: Mt. Jefferson, NV	MH	13
Gatecliff Shelter, Toquima Range, NV: Strata 31–32 (13)	39.00	116.47	2319	30: Mt. Jefferson, NV	MH	13
Gatecliff Shelter, Toquima Range, NV: Stratum 33 (13)	39.00	116.47	2319	30: Mt. Jefferson, NV	MH	13
Gatecliff Shelter, Toquima Range, NV: Stratum 37 (13)	39.00	116.47	2319	30: Mt. Jefferson, NV	MH	13
Gatecliff Shelter, Toquima Range, NV: Stratum 54 (13)	39.00	116.47	2319	30: Mt. Jefferson, NV	MH	13
Gatecliff Shelter, Toquima Range, NV: Stratum 56 (13)	39.00	116.47	2319	30: Mt. Jefferson, NV	MH	13
Garrison 1, Snake Valley, UT (14)	38.57	114.03	1640	115: Current Mountain, NV	LW	9
Garrison 2, Snake Valley, UT (14)	38.57	114.03	1640	115: Current Mountain, NV	LW	9
Snake Creek Burial Cave, Snake Valley, NV (15)	38.55	114.04	1731	115: Current Mountain, NV	LW	14
Owl Cave 2, Snake Valley, NV: Level 2 (16)	38.54	114.03	1700	115: Current Mountain, NV	LW	15
Owl Cave 2, Snake Valley, NV: Level 4 (16)	38.54	114.03	1700	115: Current Mountain, NV	LW	15
Owl Cave 2, Snake Valley, NV: Level 5 (16)	38.54	114.03	1700	115: Current Mountain, NV	LW	15
Owl Cave 2, Snake Valley, NV: Level 9 (16)	38.54	114.03	1700	115: Current Mountain, NV	LW	15
Rock Shelter, Mineral Mountains, UT (17)	38.33	112.49	1886	45: Britts Meadows, UT	ND	16
Corral North, White Mountains, CA (18)	37.34	118.13	3350	0.0: Site Vicinity	LH	17
Corral South, White Mountains, CA (18)	37.34	118.13	3350	0.0: Site Vicinity	LH	17
Enfield, White Mountains, CA (18)	37.34	118.14	3170	0.0: Site Vicinity	LH	17
Midway, White Mountains, CA (18)	37.34	118.13	3440	0.0: Site Vicinity	LH	17
Rancho Deluxe, White Mountains, CA (18)	37.29	118.14	3560	0.0: Site Vicinity	LH	17

Table 1 *continued*

Site and excavation level (if appropriate)	Latitude	Longitude	Elevation	Distance to nearest extant population (km)	Age*	Source†
Crooked Forks, White Mountains, CA (18)	37.29	118.13	3150	0.0: Site Vicinity	LH	17
Eleana Range 2–7, Eleana Range, NV (19)	37.07	116.14	1810	185: Greenmonster Canyon, NV	LW	12
Eleana Range 2–10, Eleana Range, NV (19)	37.07	116.14	1810	185: Greenmonster Canyon, NV	LW	12
Eleana Range 2–11r, Eleana Range, NV (19)	37.07	116.14	1810	185: Greenmonster Canyon, NV	LW	12
Eleana Range 3–10, Eleana Range, NV (19)	37.07	116.13	1800	185: Greenmonster Canyon, NV	LW	12
Mormon Mountain Cave, Mormon Mountain, NV (20)	37.01	114.27	1372	180: Brian Head, UT	LW	18
Fortymile Canyon 11, Yucca Mountain, NV (21)	36.57	116.22	1310	175: Cottonwood Lakes, CA	LW	12
Pintwater Cave, Pintwater Range, NV: Unit 3, Level 2 (22)	36.48	115.34	1268	260: Brian Head, UT	MH	19
Pintwater Cave, Pintwater Range, NV: Unit 3, Level 4 (22)	36.48	115.34	1268	260: Brian Head, UT	EH	19
Pintwater Cave, Pintwater Range, NV: Unit 3, Level 5 (22)	36.48	115.34	1268	260: Brian Head, UT	LW	19
Spires 2, Sheep Range, NV (23)	36.35	115.18	2040	250: Brian Head, UT	LW	12
Flaherty Mesa FM1, Sheep Range, NV (23)	36.30	115.14	1770	250: Brian Head, UT	LW	12
Willow Wash 4E, Sheep Range, NV (23)	36.28	115.15	1585	255: Brian Head, UT	LW	12
Penthouse 1, Sheep Range, NV (23)	36.28	115.15	1600	255: Brian Head, UT	LW	12
Corn Creek PR3, Las Vegas Valley, NV (24)	36.20	115.20	1060	260: Cottonwood Lakes, CA	LW	12
Potosi Mountain 2A1, Spring Range, NV (25)	36.00	115.23	1880	260: Cottonwood Lakes, CA	LW	20
Potosi Mountain 2A2, Spring Range, NV (25)	36.00	115.23	1880	260: Cottonwood Lakes, CA	LW	20
Potosi Mountain 2C2, Spring Range, NV (25)	36.00	115.23	1880	260: Cottonwood Lakes, CA	LW	20
Mescal Cave, Mescal Range, CA (26)	35.27	115.32	1550	270: Cottonwood Lakes, CA	LW	21
Antelope Cave, Ivanpah Mountains, CA (27)	35.27	115.32	1768	270: Cottonwood Lakes, CA	LW	22
Kokoweef Cave, Ivanpah Mountains, CA (28)	35.25	115.30	1770	275: Cottonwood Lakes, CA	LW	23

*LW, late Wisconsinan; EH, early Holocene; MW, middle Holocene; LH, late Holocene; ND, age unclear.

†Key to sources: 1: Grayson (1979), Jenkins *et al.* (2002); 2: Shutler & Shutler (1963); 3: Grayson & Parmalee (1988); 4: Rhode & Madsen (1995); 5: Dively-White (1989, 1990), White (1991); 6: Spiess (1974); 7: Hockett & Dillingham (2004); 8: Livingston (1992); 9: Thompson & Mead (1982); R. S. Thompson, pers. comm.; 10: Heaton (1985); 11: Miller (1979), Mead *et al.* (1982); 12: Mead & Spaulding (1995); http://climchange.cr.usgs.gov/data/midden/; 13: Grayson (1983); 14: J. I. Mead, pers. comm.; 15: Turnmire (1987); 16: Schmitt & Lupo (1995), D. N. Schmitt, pers. comm.; 17: Grayson (1991); 18: Jefferson (1982); 19: Hockett (2000); http://climchange.cr.usgs.gov/data/midden/; 20: Mead & Murray (1991); 21: Jefferson (1991); 22: Reynolds *et al.* (1991a), FAUNMAP Working Group (1994); 23: Goodwin & Reynolds (1989), Reynolds *et al.* (1991b), FAUNMAP Working Group (1994).

calculated from latitudes and longitudes using the Inverse software available from the National Geodetic Survey (http://www.ngs.noaa.gov) and were rounded to the nearest 5 km.

INCREASING ELEVATIONS AND CONTRACTING RANGES OF NOW-EXTINCT PIKA POPULATIONS

The argument that pikas colonized areas within the Great Basin during the Pleistocene and have been isolated since that time (Brown, 1971, 1978) has strong conceptual and empirical support (Grayson, 1993). That support includes the fact that, unlike the case for some other small mammals in this region (e.g. Grayson, 2000), there is no evidence that pikas recolonized any area within the prehistoric Great Basin after extirpation. As a result, it can be assumed that each Great Basin site that documents the former presence of pikas also documents their presence in that location continuously from Pleistocene times onwards. Figure 2 uses this assumption to reconstruct the geographic march of pika extinction through time in the Great Basin. This figure includes all assemblages listed in Table 1 except for those that cannot be assigned to even broad temporal categories (late Wisconsinan, *c.* 40,000–10,000 years ago; early Holocene, *c.* 10,000–7500 years ago; middle Holocene, *c.* 7500–4500 years ago; late Holocene, *c.* 4500–200 years ago).

The maps show the loss of nearly all southern and east-central Great Basin pika populations at the end of the Pleistocene, although the exact timing of that loss is not known. Given this history, the early and middle Holocene presence of pikas at Pintwater Cave, southern Nevada (Fig. 1, site 22), seems odd; the four specimens involved should be directly dated to determine whether or not the ages suggested by their stratigraphic position are correct. Perhaps most importantly, by *c.* 4500 years ago, the distribution of pikas in the Great Basin had become much as it was during historic times.

The average minimum elevation of the 18 extant Great Basin pika populations surveyed by Beever *et al.* (2003) is 2533 ± 318 m. During the late Wisconsinan and early Holocene, now-extinct pika populations occurred at an average elevation of 1750 m (1752 ± 222 and 1733 ± 308 m, respectively; see Fig. 3), a difference of 783 m. The low elevations at which late Wisconsinan and early Holocene Great Basin pika populations were found is fully consistent with empirical evidence suggesting cooler temperatures and higher effective

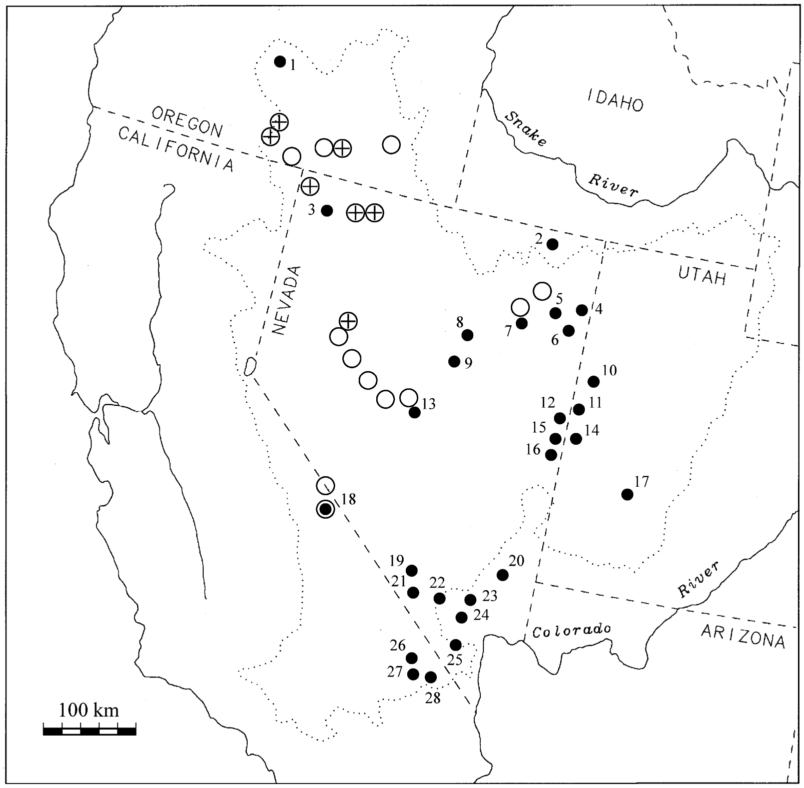

Figure 1 American pika locations within the Great Basin. Closed circles = prehistoric sites (see Table 1 for key to site numbers). Large open circles = extant populations; large open circles with crosses = populations lost during historic times (each circle may represent more than one population); populations in the Sierra Nevada and Rocky Mountains are not plotted (after Beever *et al.*, 2003). The boundary of the hydrographic Great Basin is indicated by the dotted line.

moisture during much, if not all, of this time (Grayson, 1993, 2000; Rhode & Madsen, 1995; Wigand & Rhode, 2002).

Of the 40 late Wisconsinan records for pikas in the Great Basin, 20 are based on fecal pellets from *Neotoma* middens (see Table 1). The average elevation of these middens is 1753 m, compared with an average elevation of 1751 m for the 20 late Wisconsinan sites that provided pika skeletal remains. The virtual identity of these elevations supports the argument, made above, that the use of standard archaeological and palaeontological skeletal material in this analysis has not biased the results.

The middle Holocene in the Great Basin was, on the whole, distinctly warm and dry (Grayson, 1993, 2000; Benson *et al.*, 2002; Wigand & Rhode, 2002). This climate regime is reflected by a 435 m increase in the average elevation of now-extinct pika populations, to 2168 ± 348 m, an increase that reflects the extinction of remaining lower-lying pika populations across much of the Great Basin. By the time we enter the prehistoric late Holocene, the record for extinct pika populations has become understandably sparse: there are only two stratigraphically separate records from a single site known, and this site (Gatecliff Shelter: Fig. 1, site 13) is in a range that still supports pikas at higher elevations. Other late Holocene records, from the White Mountains of California (Fig. 1, site 18), are from areas in which pikas still exist (Table 1).

The direct observational record for Great Basin pikas shows a similar process in action. The average minimum elevation of the 25 historically known pika populations in the Great Basin surveyed by Beever *et al.* (2003) is 2381 ± 401 m. As I have noted, the average minimum elevation of the 18 surviving populations is 2533 ± 318 m, a difference of 152 m.

These calculations were made by treating each stratigraphically distinct record for pikas as a separate case, since each samples a different location, a different time, or both. If stratigraphic distinctions within sites are ignored, then the results for the late Wisconsinan (1744 m), early Holocene (1724 m) and late Holocene (2319 m) are identical, or nearly so, to the results obtained when stratigraphically distinct samples are included. However, the average middle Holocene elevation falls to 1816 m, since the Gatecliff Shelter, Nevada, records now play a diminished role. Either way, the total increase in average pika elevations from the late Wisconsinan and early Holocene to today is *c.* 800 m.

In sum, the history of Great Basin pikas during the last 8000 years or so can be seen in part as a relentless loss of lower elevation populations, creating the extremely patchy, and generally high elevation, distribution seen today.

As local populations of pikas became extinct in the Great Basin, not only did the remaining populations become confined to increasingly higher elevations, but their distribution across the region constricted dramatically (Fig. 2). The magnitude of this constriction can be measured by calculating the distances between now-extinct populations and those that still exist. During the late Wisconsinan, now-extinct pika populations were located an average of 170 km from the nearest extant population (Fig. 4). By the late Holocene, this distance had declined to *c.* 30 km.

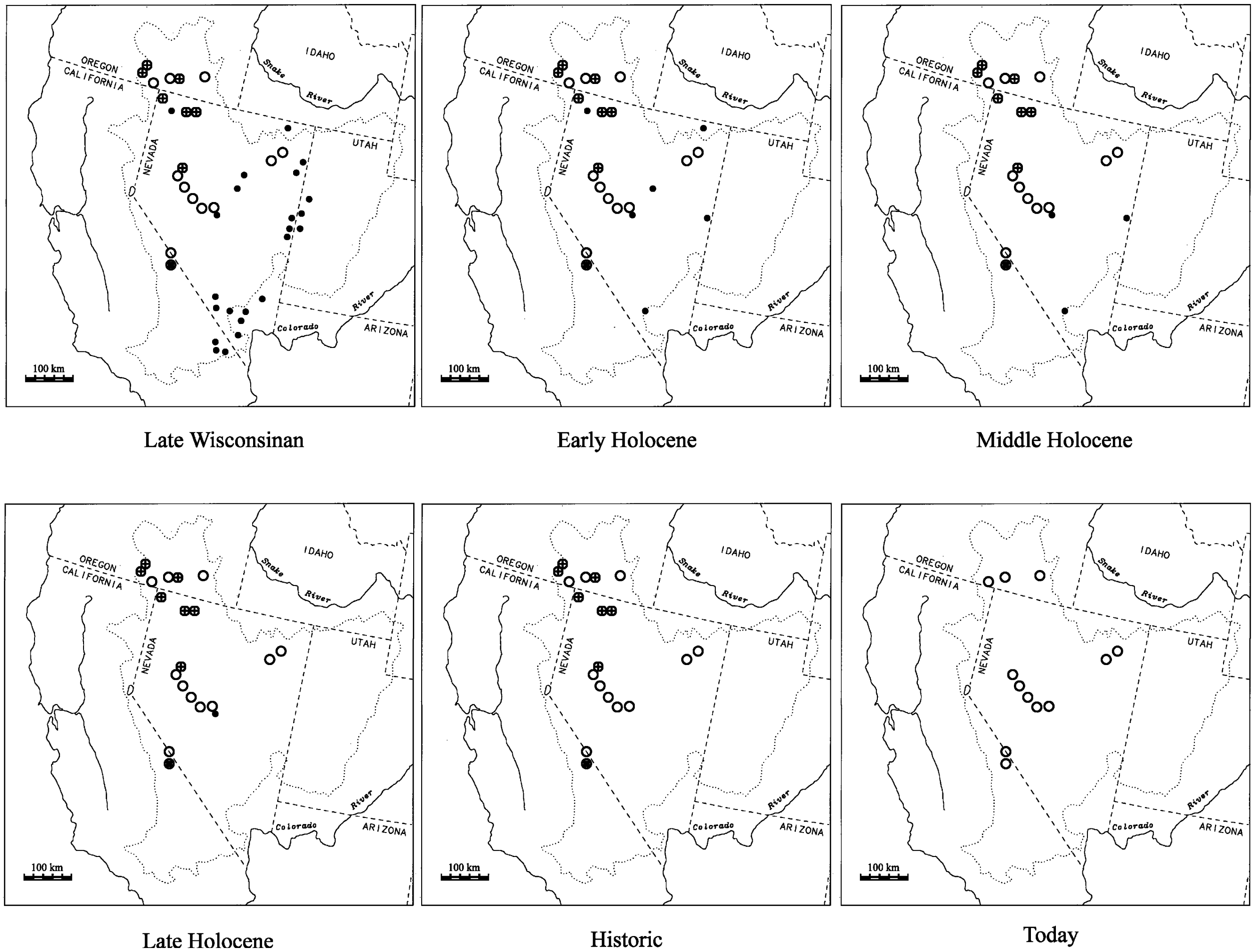

Figure 2 The extinction of pika populations through time in the Great Basin. See Fig. 1 for key.

CONCLUSIONS

These results join analyses of very different sorts (McDonald & Brown, 1992; Beever *et al.*, 2003) to suggest that the future of pikas in the Great Basin under conditions of global warming is markedly insecure. In addition to providing this subjective lesson, however, they provide a deeper historical context for the important analysis of pika extirpation provided by Beever *et al.* (2003), and by so doing, allow some refinements to their conclusions.

First, Beever *et al.* (2003, p. 48) argue that "warmer temperatures seem likely to be contributing to apparent losses that have occurred at a pace significantly more rapid than that suggested by the palaeontological records". It is true that there is nothing in the palaeontological record that suggests the loss of > 25% (7/25) of existing Great Basin pika populations within the span of a few decades. However, this may simply reflect the fact that the palaeontological record lacks the chronological precision of the historic one. Only a finer-grained record will reveal whether losses of equal magnitude and speed occurred prehistorically. Even if such losses did happen, they would have occurred at a time when Great Basin pika populations were far more abundant than they are today, and would thus not have moved them as close to extinction as they now are.

Second, the multivariate analysis of pika persistence in the Great Basin provided by Beever *et al.* (2003) demonstrates that multiple factors are likely to have caused pika extinction in this region during recent decades. In addition to such 'natural' factors as talus patch size, elevation and temperature, they document that such anthropogenic factors as distance to nearest roads and, perhaps, grazing status have played a role in driving pika losses. While it is certainly possible that humans played a role in determining aspects of past pika history in the Great Basin (e.g. Grayson, 2001), anthropogenic factors of the sort examined by Beever *et al.* (2003) are obviously not an issue for the prehistoric records assessed here. Instead, combined with the results of their important work, the prehistory of pikas in the Great Basin makes it fairly clear that their conclusion that "current anthropogenic influences … may have combined with factors operating over longer timescales (e.g. climate, habitat area) to produce fairly rapid extirpations of pikas in the Great Basin" (Beever *et al.*, 2003, p. 50) is in need of some minor modification. The prehistoric

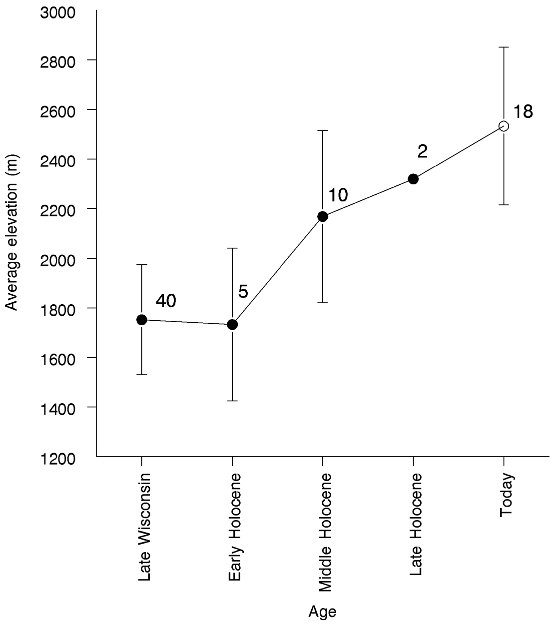

Figure 3 The changing elevations of now-extinct pika populations (solid circles) through time in the Great Basin compared with extant populations (open circle); elevations for historically described populations are minimum altitudes provided by Beever *et al.* (2003). The numbers above the symbols refer to the sample sizes used to calculate each value; error bars are plotted at one standard deviation.

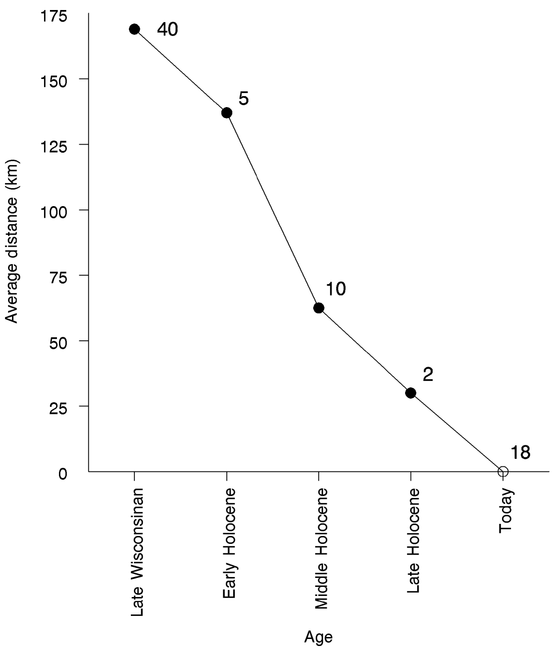

Figure 4 The changing distances between now-extinct pika populations (solid circles) and extant populations (open circle) through time in the Great Basin. The numbers above the symbols refer to the sample sizes used to calculate each value.

record of these animals leaves no doubt that anthropogenic influences *have* combined with these other variables to produce the diminished distribution that marks Great Basin pikas today. The impact that prehistoric non-anthropogenic factors have had on those animals makes controlling our current impacts on them all that more important.

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REFERENCES

Beever, E.A., Brussard, P.F. & Berger, J. (2003) Patterns of apparent extinction among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. *Journal of Mammalogy*, **84,** 37–54.

Benson, L.V., Kashgarian, M., Rye, R., Lund, S., Paillet, F., Smoot, J., Kester, C., Mensing, S., Meko, D. & Lindström, S. (2002) Holocene multidecadal and multicentennial droughts affecting northern California and Nevada. *Quaternary Science Reviews*, **21,** 659–682.

Bole, B.P., Jr (1938) Some high altitude records for mammals in the Inyo-White mountains of California. *Journal of Mammalogy*, **19,** 245–246.

Brown, J.H. (1971) Mammals on mountaintops: nonequilibrium insular biogeography. *American Naturalist*, **105,** 467–478.

Brown, J.H. (1978) The theory of insular biogeography and the distribution of boreal birds and mammals. *Intermountain biogeography: a symposium* (ed. by K.T. Harper and J.L. Reveal), *Great Basin Naturalist Memoirs* **2,** 209–227.

Dively-White, D.V. (1989) Late Quaternary zoogeography of the Toano Range based on Mad Chipmunk Cave, Elko County, Nevada. *Journal of Vertebrate Paleontology*, **9,** 19A.

Dively-White, D.V. (1990) Mad Chipmunk Cave faunule: a late Pleistocene–late Holocene record for the north-central Great Basin. *Journal of Vertebrate Paleontology*, **10,** 20A–21A.

Durrant, S.D. (1952) Mammals of Utah: taxonomy and distribution. *University of Kansas Publications, Museum of Natural History*, **6,** 1–549.

FAUNMAP Working Group (1994) FAUNMAP: a database documenting late Quaternary distributions of mammal species in the United States. *Illinois State Museum Scientific Papers*, **25,** 1–690.

Goodwin, H.T. & Reynolds, R.E. (1989) Late Quaternary Sciuridae from Kokoweef Cave, San Bernardino County, California. *Bulletin of the Southern California Academy of Sciences*, **88,** 21–32.

Grayson, D.K. (1977) On the Holocene history of some Great Basin lagomorphs. *Journal of Mammalogy*, **58,** 507–513.

Grayson, D.K. (1979) Mt. Mazama, climatic change, and Fort Rock Basin archaeofaunas. *Volcanic activity and human* *ecology* (ed. by P.D. Sheets and D.K. Grayson), pp. 427–458. Academic Press, New York.

Grayson, D.K. (1983) The paleontology of Gatecliff Shelter: small mammals. The Archaeology of Monitor Valley. 2. Gatecliff Shelter (ed. by D.H. Thomas) *American Museum of Natural History Anthropological Papers*, **59,** 98–126.

Grayson, D.K. (1987) The biogeographic history of small mammals in the Great Basin: observations on the last 20,000 years. *Journal of Mammalogy*, **68,** 359–375.

Grayson, D.K. (1991) Alpine faunas from the White Mountains, California: adaptive change in the late prehistoric Great Basin? *Journal of Archaeological Science*, **18,** 483–506.

Grayson, D.K. (1993) *The desert's past: a natural prehistory of the Great Basin*. Smithsonian Institute Press, Washington, DC.

Grayson, D.K. (2000) Mammalian responses to Middle Holocene climatic change in the Great Basin of the western United States. *Journal of Biogeography*, **27,** 181–192.

Grayson, D.K. (2001) The archaeological record of human impacts on animal populations. *Journal of World Prehistory*, **15,** 1–68.

Grayson, D.K. & Parmalee, P.W. (1988) Hanging Rock Shelter. Danger Cave, Last Supper Cave, Hanging Rock Shelter: The Faunas (ed. by D.K. Grayson) *American Museum of Natural History Anthropological Papers*, **6,** 105–115.

Grinnell, J. (1918) Six new mammals from the Mohave Desert and Inyo regions of California. *University of California Publications in Zoology*, **17,** 423–430.

Hafner, D.J. (1993) North American pika (*Ochotona princeps*) as a late Quaternary biogeographic indicator species. *Quaternary Research*, **39,** 373–380.

Hafner, D.J. (1994) Pikas and permafrost: post-Wisconsin zoogeography of *Ochotona* in the southern Rocky Mountains, U.S.A. *Arctic and Alpine Research*, **26,** 375–382.

Hall, E.R. (1946) *Mammals of Nevada*. University of California Press, Berkeley.

Hall, E.R. (1951) A synopsis of the North American Lagomorpha. *University of Kansas Publications, Museum of Natural History*, **5,** 1–202.

Heaton, T.H. (1985) Quaternary paleontology and paleoecology of Crystal Ball Cave, Millard County, Utah: with emphasis on mammals and description of a new species of fossil skunk. *Great Basin Naturalist*, **45,** 337–390.

Hockett, B.S. (2000) Paleobiogeographic changes at the Pleistocene–Holocene boundary near Pintwater Cave, southern Nevada. *Quaternary Research*, **53,** 263–269.

Hockett, B.S. & Dillingham, E. (2004) *Paleontological investigations at Mineral Hill Cave*. Contributions to the Study of Cultural Resources Technical Report, 18. U.S. Department of the Interior Bureau of Land Management, Reno, Nevada.

Howell, A.H. (1924) Revision of the American pikas. *North American Fauna*, **47,** 1–57.

Jefferson, G.T. (1982) Late Pleistocene vertebrates from a Mormon Mountain Cave in southern Nevada. *Bulletin of the Southern California Academy of Sciences*, **81,** 121–127.

Jefferson, G.T. (1991) Rancholabrean age vertebrates from the southeastern Mojave Desert, California. *Crossing the borders: Quaternary studies in eastern California and southwestern Nevada* (ed. by R.E. Reynolds), pp. 163–176. San Bernardino County Museum Association, Redlands, CA.

Jenkins, D.L., Aikens, C.M. & Cannon, W.J. (2002) *Reinvestigation of the Connley Caves 35LK50): a pivotal early Holocene site in the Fort Rock Basin of south-central Oregon*. Manuscript on file at the University of Oregon Museum of Natural History, Eugene.

Livingston, S.D. (1992) Mammals of Serendipity Cave and the Roberts Mountains. *Paper Presented at the 1992 Great Basin Anthropological Conference*, Boise, ID.

McDonald, K.A. & Brown, J.H. (1992) Using montane mammals to model extinctions due to global change. *Conservation Biology*, **6,** 409–415.

Mead, J.I. (1987) Quaternary records of pika, *Ochotona*, in North America. *Boreas*, **16,** 165–171.

Mead, J.I. & Grady, F. (1996) *Ochotona* (Lagomorpha) from late Quaternary cave deposits in eastern North America. *Quaternary Research*, **45,** 93–101.

Mead, J.I. & Murray, L.K. (1991) Late Pleistocene vertebrates from the Potosi Mountain packrat midden, Spring Range, Nevada. *Crossing the borders: Quaternary studies in eastern California and southwestern Nevada* (ed. by R.E. Reynolds), pp. 124–126. San Bernardino County Museum Association, Redlands, CA.

Mead, J.I. & Spaulding, W.G. (1995) Pika (*Ochotona*) and paleoecological reconstructions of the Intermountain West, Nevada and Utah. Late Quaternary environments and deep history: a tribute to Paul S. Martin (ed. by D.W. Steadman and J.I. Mead). *The Mammoth Site of Hot Springs, South Dakota Scientific Paper*, **3,** 165–186.

Mead, J.I., Thompson, R.S. & Van Devender, T.R. (1982) Late Wisconsinan and Holocene fauna from Smith Creek Canyon, Snake Range, Nevada. *Transactions of the San Diego Society of Natural History*, **20,** 1–26.

Miller, S.J. (1979) The archaeological fauna of four sites in Smith Creek Canyon. The archaeology of Smith Creek Canyon, Eastern Nevada (ed. by D.R. Tuohy and D.L. Rendall). *Nevada State Museum Anthropological Papers*, **17,** 272–331.

Reynolds, R.E., Reynolds, R.L., Bell, C.J. & Pitzer, B. (1991a) Vertebrate remains from Antelope Cave, Mescal Range, San Bernardino County, California. *Crossing the Borders: Quaternary Studies in Eastern California and southwestern Nevada* (ed. by R.E. Reynolds), pp. 107–109. San Bernardino County Museum Association, Redlands, CA.

Reynolds, R.E., Reynolds, R.L., Bell, C.J., Czaplewski, N.J., Goodwin, H.T., Mead, J.I. & Roth, B. (1991b) The Kokoweef Cave faunal assemblage. *Crossing the borders: Quaternary studies in eastern California and southwestern Nevada* (ed. by R.E. Reynolds), pp. 97–103. San Bernardino County Museum Association, Redlands, CA.

Rhode, D. & Madsen, D.B. (1995) Early Holocene vegetation in the Bonneville Basin. *Quaternary Research*, **44,** 246–256.

Schmitt, D.N. & Lupo, K.D. (1995) On mammalian taphonomy, taxonomic diversity, and measuring subsistence data in zooarchaeology. *American Antiquity*, **60,** 496–514.

Shutler, M.E. & Shutler, R., Jr (1963) Deer Creek Cave, Elko County, Nevada. *Nevada State Museum Anthropological Papers*, **11,** 1–70.

Smith, A.T. (1974a) The distribution and dispersal of pikas: consequences of insular population structure. *Ecology*, **55,** 1112–1119.

Smith, A.T. (1974b) The distribution and dispersal of pikas: influences of behavior and climate. *Ecology*, **55,** 1368–1376.

Smith, A.T. & Weston, M.L. (1990) Ochotona princeps. *Mammalian Species*, **352,** 1–8.

Spiess, A. (1974) Faunal remains from Bronco Charlie Cave (26EK801), Elko County, Nevada. *The prehistoric human ecology of southern Ruby Valley, Nevada* (ed. by L.A. Casjens), pp. 452–486. PhD Dissertation, Harvard University, Cambridge.

Thompson, R.S. & Mead, J.I. (1982) Late Quaternary environments and biogeography in the Great Basin. *Quaternary Research*, **17,** 35–39.

Turnmire, K.L. (1987) An analysis of the mammalian fauna from Owl Cave One and Two, Snake Range, east-central Nevada. MS Thesis, University of Maine, Orono.

Verts, B.J. & Carraway, L.N. (1998) *Land mammals of Oregon*. University of California Press, Berkeley.

White, S.R. (1991) Late Quaternary paleobotany at Mad Chipmunk Cave, Elko County, Nevada. MS Thesis, Northern Arizona University, Flagstaff.

Wigand, P.E. & Rhode, D. (2002) Great Basin vegetational history and aquatic systems. *Great Basin aquatic systems history* (ed. by R. Hershler, D.B. Madsen and D.R. Currey). *Smithsonian Contributions to the Earth Sciences*, **33,** 309–368.

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