Western North American Naturalist 81(2), © 2021, pp. 141–170

Camera traps provide insights into American pika site occupancy, behavior, thermal relations, and associated wildlife diversity

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ABSTRACT.—Custom camera traps were positioned at American pika (*Ochotona princeps*) haypiles in 12 warm, low-elevation locations of eastern California over 5 years and during warm and cold seasons. These camera traps detected 26 mammal and 10 bird species, including 4331 pika events as well as visits by 16 sympatric herbivores and 7 pika predators. Camera traps documented pika occupancy at some sites that had been evaluated from field surveys as extirpated, and they also confirmed field assessments of extirpation at other sites. Individual pikas could be distinguished by scars, size, and pelage diagnostics, allowing animals to be followed through sequences of photos and enabling behavioral interpretations and documentation of winter and warm-season activities. Temperature measurements at haypiles and talus interiors corroborated prior findings that rocky interiors are much cooler than surfaces, have highly attenuated daily temperature fluctuations, and offer refuge for pikas from high daytime temperatures. Nocturnal activity was recorded for pikas as well as for many other species, but we found little evidence that night activity of pikas at haypiles increased when prior day temperatures were excessively warm. The capacity of pikas to be active at all times of the day adds to their resilience in the face of predators, foraging needs, and changing climates.

RESUMEN.—Colocamos cámaras trampa personalizadas cerca de pilas de heno para observar la pika americana (*Ochotona princeps*) en 12 lugares cálidos y de baja elevación del este de California durante cinco años y durante las estaciones cálidas y frías, y detectamos 26 especies de mamíferos y 10 de aves. Estos incluyeron 4331 eventos de pika, así como visitas de 16 herbívoros simpátricos y 7 depredadores de la pika. Las cámaras trampa documentaron la ocupación en algunos sitios que habían sido evaluados a partir de estudios de campo como extirpados, y confirmaron evaluaciones de campo de la extirpación en otros sitios. Las pikas individuales se pueden distinguir por las cicatrices, el tamaño y el diagnóstico del pelaje. Nuestros diagnósticos de identificación de la pika nos permitieron seguir a los animales a través de secuencias de fotos, realizar interpretaciones de comportamientos y nos ayudaron a documentar tanto las actividades invernales como las de la estación cálida. Las mediciones de temperatura en montones de heno e interiores de talud corroboraron hallazgos anteriores de que los interiores rocosos son mucho más fríos que las superficies, tienen fluctuaciones diarias muy atenuadas y ofrecen refugio a las pikas de las altas temperaturas diurnas. Se registró actividad nocturna para las pikas así como para muchas otras especies, pero encontramos poca evidencia de que la actividad nocturna de pikas en pilas de heno aumentaba cuando las temperaturas del día anterior eran excesivamente cálidas. La capacidad de las pikas para estar activas en todo momento del día se suma a su resistencia frente a los depredadores, las necesidades de alimentación y los climas cambiantes.

American pikas (*Ochotona princeps*, order Lagomorpha) are small montane mammals, wide-ranging across western North America, that have drawn attention for their apparent sensitivity to warming climates (Beever et al. 2003, 2011, Grayson 2005). Conditions that predispose them to vulnerability include poor thermoregulation, low lethal body temperature, low fecundity, nonhibernating habit, solitary and crepuscular behavior, small population size, and limited dispersal capacity (Smith 1974, Smith and Weston 1990). Despite these factors, contrasting conditions of persistence in the face of changing climates have been reported across the species' range, including within single bioregions. Studies in the Great Basin in particular have documented populations that are rapidly declining or recently extirpated (Beever et al. 2003, 2011, Wilkening et al. 2011, Jeffress et al. 2017) as well as populations that appear to be stable (Beever et al. 2008, 2011, Millar and Westfall 2010,

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Millar et al. 2013, 2018, Smith et al. 2016, Jeffress et al. 2017).

Pikas are restricted to habitats of shattered rock slopes, including talus, lava flows, and eroding bedrock (collectively, "talus") that lack fine sediments, have clasts 0.2 m to 1 m in diameter, and have open voids between rocks (Smith and Weston 1990). Persistence of populations, despite increasing regional air temperature, appears at least partly related to the cool microclimates of the talus interiors. Taluses develop unique air circulation that cools their interiors in summer, warms them in winter, and greatly reduces diurnal extremes (Morard et al. 2010, Millar et al. 2014b). Behavioral adaptation, combined with the presence of such "air-conditioned" taluses, is thought to contribute to pika persistence despite the species' thermal sensitivity (Smith 1974, MacArthur and Wang 1974, Varner et al. 2016, Smith et al. 2016, Beever et al. 2017), but field evidence of such adaptive behavior remains circumstantial. Pikas have been observed calling and being active at night, and such activity has been considered behavioral avoidance of daytime high temperatures (Smith 1974). However, few studies of the nocturnal behavior of pikas have been conducted, and this topic deserves more research (Smith et al. 2016, Hall and Calfoun 2019, Camp et al. 2020).

Surveys of habitat occupancy are critical to assessments of population status and trend, especially in areas where concern exists about threats from climate change. Although historic use of a talus by pikas is relatively easy to verify in the field from indirect sign (e.g., Jeffress et al. 2017), current occupancy cannot always be readily or accurately determined. In addition to vocalization and direct animal sightings, traits typically used to define current occupancy include fresh fecal pellets and green vegetation in "haypiles" (i.e., caches of vegetation collected by pikas in summer for winter feeding). However, especially with rapid assessments and in areas marginal to main habitat, occupancy can be easily overlooked, and occupied taluses can be mistakenly attributed as extirpated (Smith et al. 2016, Millar et al. 2018, Camp et al. 2020).

Despite detailed descriptions of pikas' natural history, questions remain about the species' ecology in relation to its climate sensitivity, and thus uncertainties persist for assessing pika vulnerability to climate change. These uncertainties include questions of current occupancy versus extirpation history, territory turnover, seasonal talus use, diel behavior, interactions with sympatric herbivores and predators, and behavioral dynamics in response to temperature. Some of these topics are recalcitrant to traditional field methods. Camera trapping is a valuable, relatively new approach in wildlife studies with proven capacity to shed light on unsolved questions for a range of species, including pikas (Massing 2012, Li and Smith 2015, Hall and Calfoun 2019, Camp et al. 2020). Camera traps have certain benefits over trapping or direct observation, the most obvious being the opportunity for continuous monitoring over long periods (including through both day and night and during winter or inclement weather) without disturbance to wildlife or the need for human observers (Vine et al. 2009). In many situations, distinct markings on animals (pelage patterns, injuries/scars, size) enable identification of individuals in repeat photos, allowing evaluation of social dynamics and occupancy modeling (Karanth 1995).

We deployed custom camera traps adjacent to pika haypiles in talus locations along the western edge of the Great Basin to investigate whether cameras could provide new insight on pika status and ecology. In particular we addressed the following questions:

1. How effective are camera traps in recording pika activity and behaviors? Can cameras provide information about pika occupancy in a talus where this information has not been resolved by field observations or where the results differ from field observations?
2. What other species visit pika haypiles, and how might they affect pika conditions?
3. What diel behavioral patterns characterize activity by pikas and other species that visit haypiles?
4. What temperatures characterize haypile sites and subsurface talus habitats? Does pika diel activity relate to temperature?

METHODS

Study Sites

We installed camera traps at 12 talus sites in Mono County, eastern California, where pikas have been observed or indication of prior use exists (Fig. 1, Table 1; Millar et al. 2013, 2018). These included 5 locations in the Sierra Nevada, 4 in the Bodie Mountains, and 3 in the Mono

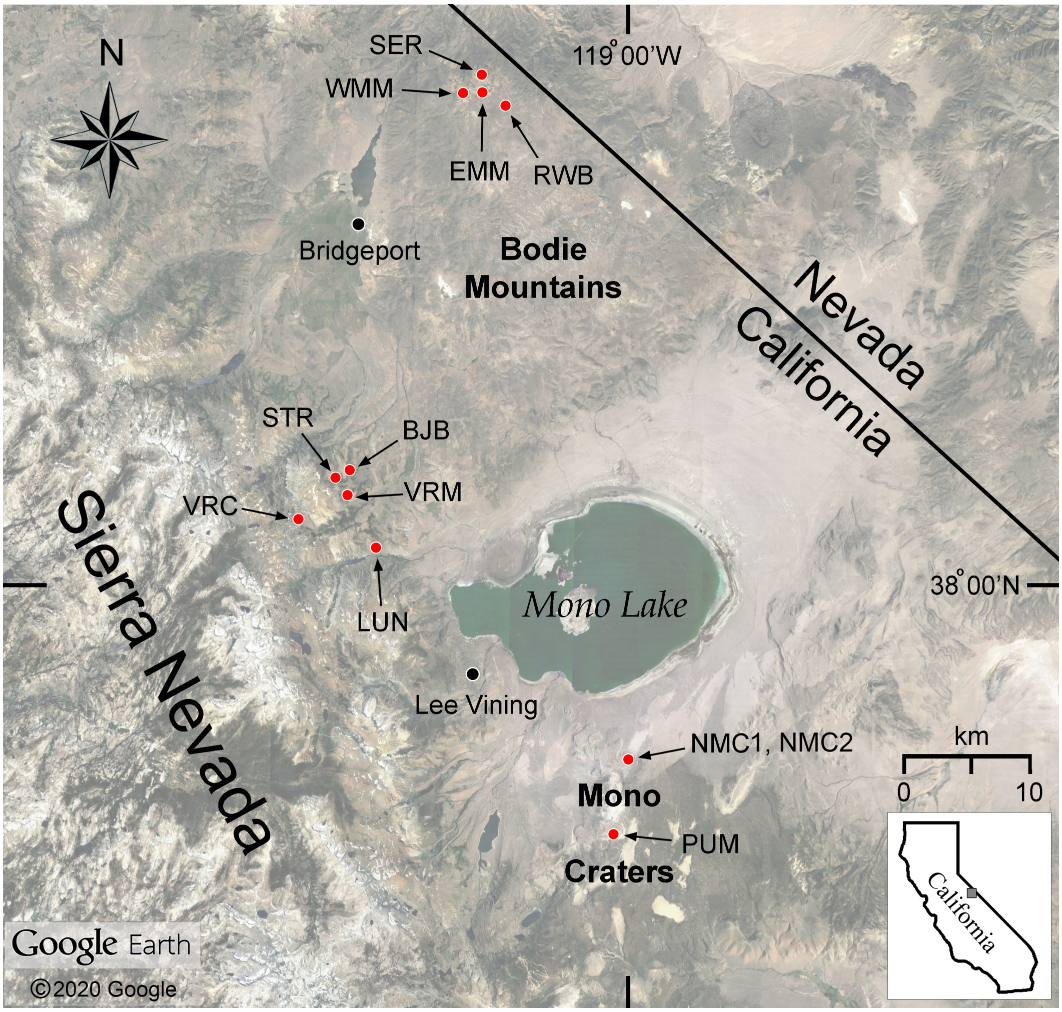

Fig. 1. Study region in eastern California showing locations of 12 talus sites where camera traps were installed at American pika haypiles.

Craters. We consider all but one site to be marginal pika habitats within the scope of western Great Basin environments. The typical pika site (Virginia Lakes Canyon; VRC) lies at 3061 m elevation in a glaciated Sierra Nevada canyon with extensive talus. The talus forefield supports subalpine meadow vegetation with graminoids and forbs; willow shrubs and subalpine forest surround the meadow. The remaining sites are relatively low, warm, and dry for pikas in this region (mean elevation, 2661 m; lowest elevation, 2216 m), and most are isolated patches of talus. The exception to isolation is the Virginia Moraine site (VRM), which lies at the base of an extensive talus slope above the left-lateral moraine of Virginia Canyon and is more or less connected to talus up-canyon.

The Bodie Mountains and Mono Craters are small outlier ranges for pikas in the Great Basin, and they have no apparent current connectivity to pika populations in the Sierra Nevada or other ranges. All but 3 sites in those ranges have south or easterly aspects, amplifying exposure to warm temperatures. Several sites exemplify extreme conditions for pikas, with talus surrounded by barren pumice forefields (Mono Craters sites) or by forefields with woody vegetation and species high in alkaloids (e.g., *Artemisia* spp.; Smith et al. 2016).

TABLE 1. Study sites in Mono County, eastern California, listed from north to south. Climate data from the PRISM model (Daly et al. 1994) extracted from the 1981 to 2010 normals. Substrate determinations are from John et al. (2015) and Kistler (1966). POR = period of record.

Site name	Site code	Pika occupancy/ year last occupied[a]	Mountain range	Latitude, longitude	Elevation (m)	Aspect	Talus substrate	Vegetation zone	Climate means	
									Temp Ann/ JulyAugSep (°C)	Precip (mm)
Serita Mine	SER	UnC/April 2012	Bodie Mtns.	38.360, −119.126	2566	N	trachyandesite	*Pinus monophylla* woodland	5.1/13.9	541
East Masonic Mtn.	EMM	UnC/April 2012	Bodie Mtns.	38.348, −119.128	2764	E	granodiorite	*P. monophylla* woodland/ *Artemisia* mixed shrub	4.7/13.4	589
West Masonic Mtn.	WMM	UnC/July 2015	Bodie Mtns.	38.346, −119.143	2724	N	granodiorite	*P. monoplylla* woodland/ *Artemisia* mixed shrub	4.9/13.6	587
Red Wash Buttes	RWB	UnC/June 2017?	Bodie Mtns.	38.339, −119.104	2747	NNW	trachyandesite	*Artemisia* mixed shrub	4.4/13.1	558
Benjamin Buttes	BJB	Occ	Sierra Nevada	38.083, −119.233	2801	E	meta-sedimentary	*P. contorta*/ *Artemisia-Ribes* mixed shrub	3.6/12.2	697
State Rocks	STR	Occ	Sierra Nevada	38.080, −119.245	3005	E	meta-sedimentary	*P. albicaulis*/ *Ribes* shrub	3.3/11.8	735
Virginia Moraine	VRM	Occ	Sierra Nevada	38.066, −119.238	2907	SE	meta-sedimentary	*P. albicaulis*/ *P. contorta* forest	2.8/11.3	807
Virginia Lakes Canyon	VRC	Occ	Sierra Nevada	38.053, −119.273	3061	SSE	meta-sedimentary	*P. albicaulis*/ *P. contorta* forest	2.0/10.2	957
Lundy Canyon	LUN	Occ	Sierra Nevada	38.035, −119.214	2367	S	meta-sedimentary	*P. jeffreyi* forest	4.8/13.5	665
Mono Craters	NMC1	UnC/March 2018?	Mono Craters	37.892, −118.997	2219	S	ryholite	*P. jeffreyi* forest	6.0/14.8	471
Mono Craters	NMC2	UnC/March 2018?	Mono Craters	37.892, −118.9965	2216	S	ryholite	*P. jeffreyi* forest	6.0/14.8	471
Pumice	PUM	Occ	Mono Craters	37.843, −119.005	2558	S	ryholite	*P. jeffreyi* forest	4.5/13.0	598

[a]Occ = recently documented occupancy. UnC = uncertain occupancy. For UnC, year last occupied is the last time occupancy was verified in the field or, if "?", date of last visit when indirect sign appeared to be ≤2 years old.

Fig. 2. Custom camera trap used for study. ***A,*** Closed camera trap showing sturdy exterior of case with lens, flash, and motion sensor. ***B,*** Case open to show camera, controller card with motion sensor, and add-on batteries for additional longevity.

Pikas in the Bodie Mountains have been the focus of the longest longitudinal study on the species (Smith and Nagy 2015). This and other work (Millar et al. 2013, 2014a, Nichols et al. 2016) have documented decline in occupancy of sites in the range over recent years, such that other than anthropogenic habitat (historic mining deposits) at Bodie State Historic Park, pikas are considered near extinct in the range (Millar et al. 2014a). Though less studied, the Mono Craters are unlikely habitat for pikas given their low elevations, volcanic talus with barren forefields, and hot environments. Smith et al. (2016) studied the southern population in the Mono Craters, which included our Pumice Mine site.

Current occupancy at 6 sites was verified by field observations that have been ongoing for more than 15 years (Table 1). At the remaining 6 sites, occupancy at the time our studies began was uncertain. All sites of current uncertain occupancy had been observed in previous years either as occupied (animal seen, calls heard, or green vegetation in haypiles) or as apparently occupied within 1–2 years of the oldest site visit. Dates of last confirmed observation of occupancy, or estimate of last occupancy for the uncertain sites, are given in Table 1.

Camera Trapping

We used high-quality custom camera traps optimized for sensing and photographing small mammals (Fig. 2). Each handmade camera trap included a Yeticam controller card with embedded passive infrared motion sensor that was wired to a Sony or Pentax high-resolution point-and-shoot digital camera (Sony DSC-600, Sony DSC-H70, and Pentax Optio e60) and built into a rugged weatherproof Pelican™ case (Pelican Products, Inc., www.pelican.com). These components create camera traps with several key features useful for small mammal monitoring that are not generally available in commercial trail cameras: wide-angle lenses (2× the field of view of standard trail cameras), autofocusing from infinity to ~30 cm (commercial trail cameras have a fixed focus), high-speed adjustable white flash (for detailed, full-color night photos), and adjustable exposure, ISO and white balance (to optimize image quality for day and night photos). One camera was installed in talus at each of the 12 sites. Cameras were set ~0.75 m from a pika haypile,

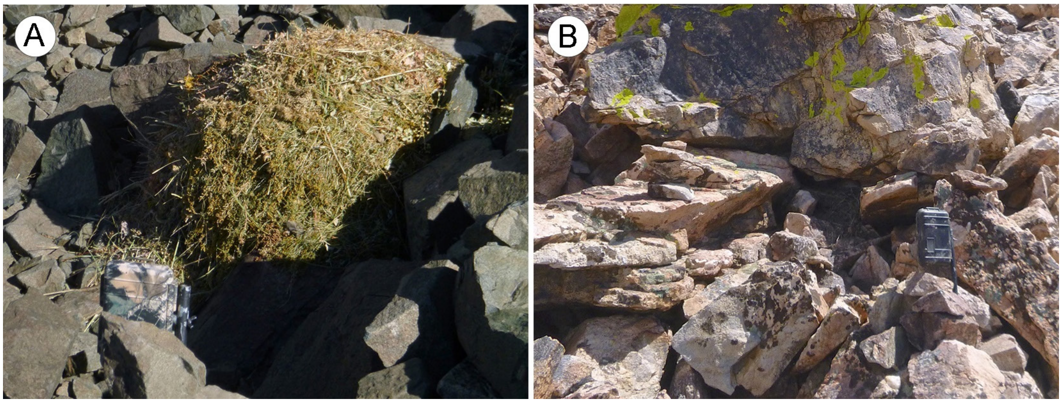

Fig. 3. Camera traps at American pika haypiles. ***A,*** Camera aimed at active haypile. ***B,*** Camera aimed at central area of an inactive haypile.

wedged into the talus on a 2-cm-diameter steel post, and situated ~30–50 cm above the ground, with the motion sensor and lens oriented toward the haypile (Fig. 3). Care was taken to position the camera so as to minimize interference from direct sunlight and to avoid deep shade on the haypiles or wind-blown plants that could cause false triggers. In the case of taluses with uncertain occupancy, the freshest-appearing haypile was chosen for observation. All cameras were provisioned with high-capacity lithium batteries that can endure temperature extremes. Each camera trap was programmed to turn on and take photos when triggered by motion in the scene, and turn off once the motion ended and the scene was motionless for 30 s. As long as batteries persisted, the cameras recorded photos until the internal storage card was full. A sampling period was one continuous duration at a location, during which a camera was actively taking photos before the batteries died, the memory card filled, the card was downloaded and batteries exchanged, or the camera was removed. Cameras were set at different times and recorded different periods and seasons over a varying number of years. The first camera was deployed on 27 September 2014, and the last camera was removed on 2 October 2019 (Table 2). Each image recorded the date and time of the photograph.

Analysis of Photographs

Records were retrieved from cameras after each sampling period, and all photographs were downloaded to a computer and organized into folders by year, site, and sampling period. Records were separated into 3 subsets per site and sampling period: photos with pikas, photos with other species, and photos with no visible animals. Species were identified by reference to diagnostic features visible in the photos (Sibley 2001, Jameson and Peeters 2004, and relevant *Mammalian Species* accounts). Not all animals in individual photos could be identified to species (e.g., only part of the animal was shown), and in these cases the animal was identified to genus only. Questionable identities were referred to experts for their opinion (Dr. James Patton, University of California, Berkeley; Dr. Andrew Smith, Arizona State University; Dr. Chris Wemmer, Smithsonian National Zoo). Pika photos were analyzed carefully for behavior, maturity (juvenile, adult), and identification of individual animals. The latter was based on distinctive characteristics visible in the high-resolution images.

Exifgrabber software was used to extract the EXIF metadata from the image files and generate spreadsheets of raw visitation data for pikas and other species for each site and sampling period, including dates and timestamps with each datum. Visitation data were analyzed to isolate and count distinct events using the following evaluation criteria: a minimum of 2 min between events, the animal leaving the scene, or the camera turning off for lack of activity. Diel activity was scored as diurnal, 8:00 to 18:00; crepuscular, 18:00 to 21:00 and 5:00 to 8:00; and nocturnal, 21:00 to 5:00.

TABLE 2. Camera trap and temperature logger metadata with summary event data. POR (period of record) = first date that camera or iButton was set to the last date removed; sampling was not always continuous. Sample period = one continuous interval of time during which the camera was actively taking photos before the batteries died, the memory card filled up, the card was downloaded and batteries exchanged, or the camera was removed. Events = total number of mammal and bird visits to haypiles recorded in photographs. See Table 1 for site names and Supplementary Material 1 for dates of each sample period.

	Camera traps					Temperature loggers
Site	POR	Sample periods	Total sample days	Total events	Mean events/ day	POR
SER	9 Jun 2017 to 11 Jul 2017	1	32	34	1.1	12 Jun 2017 to 9 Oct 2017
EMM	6 Jun 2018 to 2 Oct 2018	2	123	69	0.6	1 Jun 2018 to 1 Jun 2019
WMM	9 Jun 2017 to 2 Oct 2019	3	235	337	1.4	12 Jun 2017 to 12 Jun 2019
RWB	1 Jun 2018 to 5 Sep 2018	2	96	200	2.1	1 Jun 2018 to 1 Jun 2019
BJB	25 Jun 2016 to 18 Sep 2017	5	144	2176	15.1	26 Jun 2016 to 17 Aug 2019
STR	29 Jul 2016 to 12 Sep 2016	1	45	171	3.8	26 Jun 2016 to 14 Aug 2019
VRM	22 Jul 2015 to 2 Sep 2015	1	42	893	21.3	24 Jul 2015 to 24 Jul 2019
VRC	27 Sep 2014 to 9 Oct 2016	6	171	708	4.1	23 Jun 2014 to 24 Jul 2019
LUN	21 Apr 2015 to 18 Nov 2017	10	368	1154	3.1	21 Apr 2015 to 18 Aug 2019
NMC1	1 Jun 2018 to 28 Aug 2018	2	64	233	3.6	1 Jun 2018 to 1 Jun 2019
NMC2	16 Aug 2019 to 29 Sep 2019	1	44	42	1.0	no loggers deployed
PUM	21 Apr 2015 to 9 Oct 2015	4	145	114	0.8	7 Nov 2015 to 29 Aug 2017
TOTAL	**27 Sep 2014 to 2 Oct 2019**	**38**	**1509**	**6131**	**4.1**	**23 Jun 2014 to 18 Aug 2019**

Temperature Measurements

Temperature dataloggers (Maxim iButtons, model 1921G) were installed at all sites except NCM2 (Table 2). Loggers were programmed to record every 4 h starting at noon on the day of deployment. Units were wrapped in wire mesh and inserted with a wire tether into 4-cm white PVC "T" tubes, which acted as radiation shields and protection for the unit. At each site, one logger was positioned on the talus surface at the haypile near the camera and another in the talus matrix (0.5–1.0 m subsurface) within 2 m of the camera. Loggers were installed for varying periods of time and with different start and end dates, and they were exchanged when possible to maintain continuous logging for periods of 1 season to 5 years (Table 2). The overall temperature recording period was 23 June 2014 to 18 August 2019.

To assess the hypothesis that nocturnal pika activity increases following excessively warm daytime temperatures (e.g., Smith 1974, Massing 2012, Smith et al. 2016, Camp et al. 2020), we compared reference period temperatures with nocturnal event temperatures. Reference periods were intervals of time that contained a set of nocturnal events within sampling periods, and, where temperature data were available, extended ~7–10 d beyond the first and last nocturnal event date. We compiled the date and time for each nocturnal event and calculated the mean temperature for the warmest part of the day before the event and for the night of the nocturnal events. We compared these to temperatures during the relevant reference period, assessing mean daily temperature, daily maximum and minimum temperatures, and night temperature for the reference period.

RESULTS

Animal Diversity

Between September 2014 and October 2019, camera traps at 12 pika sites captured 27,345 photos, of which 10,336 were of pikas, 3285 were of other animals, and 13,724 showed no visible animal (false triggers or animal left scene). These photos represented 6132 unique animal events (pikas, other mammals, and birds) over 1509 sampling days (Table 2, Supplementary Material 1). All sites recorded animals, although there was large variability among sites in frequency of events and species photographed. Four sites in the Sierra Nevada (BJB, VRM, VRC, LUN) were most active, with a mean of 1232.8 events ($\bar{x}$ = 10.1 events/d), and 3 sites in the Bodie Mountains (SER, EMM, and WMM) were least active, with a mean of 48.3 total events ($\bar{x}$ = 0.9 events/d). Overall, cameras photographed 26 mammal

Fig. 4. Example images of American pika obtained from custom camera traps. ***A,*** Mature individual carrying foliage of *Veratrum californicum* (note notch in ear used for identification). ***B,*** Juvenile pika perching on rock. Visible wire is the tether for the temperature logger, which is situated below the rock.

species representing 12 families from 4 orders (Lagomorpha, Rodentia, Carnivora, and Chiroptera; Table 3). Golden-mantled ground squirrels (*Callospermophilus lateralis*) and least chipmunks (*Neotamias minimus*) were present at all sites, and deer mice (*Peromyscus maniculatus*) were present at all but one site (STR). Lodgepole chipmunks (*Neotamias speciosus*) and canyon mice (*Peromyscus crinitus*) were slightly less common, documented at 7 and 6 sites, respectively. At sites where both chipmunk and both deer mouse species were present, the 2 species could be distinguished in some but not all photos, so event counts were combined.

American pika (Fig. 4) was the fifth most common mammal photographed, occurring at 66.7% of the sites (Table 3). The long-tailed weasel (*Mustela frenata*) also occurred at 66.7% of the sites, but it was photographed far less frequently. Pikas were not documented at 4 sites: SER, EMM, RWB in the Bodie Mountains and NMC2 in the Mono Craters. All of these were initially sites of uncertain occupancy based on field observations. Unsurprisingly, with the cameras focused on haypile sites, pikas were by far the most frequently photographed animal, accounting for 71% of the total animal events and 76% of the animal photos. Pikas were most commonly photographed at Sierra Nevada locations, with BJB (1772), VRM (849), and LUN (846) recording the largest number of pika events, and NMC1 (3) and PUM (22) in the Mono Craters the least (Table 3). Pikas were photographed at sites where occupancy based on field observations was uncertain, including WMM in the Bodie Mountains and NMC1 in the Mono Craters.

Several uncommon species, or species not expected in talus habitat, were photographed (Table 3). Among Rodentia, these included the mountain pocket gopher (*Thomomys monticola*) at VRC in the Sierra Nevada; sagebrush vole (*Lemmiscus curtatus*) at EMM and WMM in the Bodie Mountains (Fig. 5); and long-tailed vole (*Microtus longicaudus*) at LUN in the Sierra Nevada. Carnivora that were less expected in talus were depicted in one photograph of an American black bear (*Ursus americanus*) at RWB in the Bodie Mountains and many images of the spotted skunk (*Spilogale gracilis*; Fig. 6), which was represented at 58% of sites from all 3 mountain regions and which was the second most commonly photographed predator. Uncommon for our region was ringtail (*Bassariscus astutus*), photographed twice at LUN in the Sierra Nevada (Fig. 6), and unexpected for the elevation and plant community was desert woodrat (*Neotoma lepida*), which was photographed at all Bodie Mountain sites with relatively high frequency (Fig. 5). Pine marten (*Martes americana*), bobcat (*Lynx rufus*) and gray fox (*Urocyon cinereoargenteus*), while common in the region, were not expected to be represented as abundantly in talus environments (8%–33% of sites; Fig. 6). The single bat species recorded, long-eared bat (*Myotis evotis*), occurred in relatively high frequency (29 events in only 64 sample days) at NMC1

TABLE 3. Mammals and birds photographed by camera traps at 12 American pika haypile sites, 2014–2019. See Table 1 for site names. Events = total number of visits to haypiles recorded in photographs for each species. Sites = total number and percentage of haypile sites each species documented. Noct = nocturnal events recorded between 21:00 and 05:00.

		Number of photographic events by site												Sites total		Events total noct	
		Bodie Mountains				Sierra Nevada					Mono Craters						
Taxon	Common name	SER	EMM	WMM	RWB	BJB	STR	VRM	VRC	LUN	NMC1	NMC2	PUM	*n*	%	*n*	%
MAMMALS																	
Lagomorpha																	
Ochotonidae																	
Ochotona princeps	American pika			139		1772	133	849	567	846	3		22	8	67	4331	15
Leporidae																	
Sylvilagus nuttallii	Mountain cottontail	2	10		7	1		1		6				6	50	27	33
Rodentia																	
Sciuridae																	
Marmota flaviventris	Yellow-bellied marmot			19	3	1	9		23	2				6	50	57	0
Callospermophilus lateralis	Golden-mantled ground squirrel	2	12	33	34	132	15	21	5	4	39	3	9	12	100	309	0
Otospermophilus beecheyi	California ground squirrel			1	5	9				31				4	33	46	0
Urocitellus beldingi	Belding's ground squirrel			1		4	4		15					4	33	24	0
Tamiasciurus douglasii	Douglas's squirrel					2			17		3		8	4	33	30	0
Neotamias minimus	Least chipmunk[a]	3	5	16	27	62	1	13	21	11	75	3	14	12	100	251	0
Neotamias speciosus	Lodgepole chipmunk[a]													7	58		0
Geomyidae																	
Thomomys monticola	Mountain pocket gopher								1					1	8	1	0
Heteromyidae																	
Perognathus parvus	Great Basin pocket mouse	1	2		6							3		4	33	12	100
Cricetidae																	
Lemmiscus curtatus	Sagebrush vole		1	3						1				3	25	5	100
Microtus longicaudus	Long-tailed vole									2				1	8	2	50
Neotoma cinerea	Bushy-tailed woodrat			6		29			30	125		11	49	6	50	250	99
Neotoma lepida	Desert woodrat	17	10	12	2									4	33	41	100
Peromyscus maniculatus	Deer mouse[b]	5	9	21	56	110		7	20	84	76	18	9	11	92	415	100
Peromyscus crinitus	Canyon mouse[b]													6	50		100
Carnivora																	
Ursidae																	
Ursus americanus	American black bear				1									1	8	1	0
Canidae																	
Urocyon cinereoargenteus	Gray fox		2	2						5	3			4	33	12	67
Felidae																	
Lynx rufus	Bobcat			7	1									2	17	8	63

TABLE 3. Continued

		Number of photographic events by site												Sites total		Events total noct	
		Bodie Mountains				Sierra Nevada					Mono Craters						
Taxon	Common name	SER	EMM	WMM	RWB	BJB	STR	VRM	VRC	LUN	NMC1	NMC2	PUM	*n*	%	*n*	%
Mustelidae																	
Martes americana	Pine marten								1					1	8	1	100
Mustela erminea	Short-tailed weasel		1		18	3				1				4	33	23	30
Mustela frenata	Long-tailed weasel			7	1	15	1	2	5	14			3	8	67	48	6
Spilogale gracilis	Spotted skunk	1		6	5	1				10	3	2		7	58	28	100
Procyonidae																	
Bassariscus astutus	Ringtail											2		1	8	2	100
Chiroptera																	
Vespertilionidae																	
Myotis evotis	Long-eared bat										29			1	8	29	100
TOTAL MAMMAL EVENTS														12	100	5953	25
BIRDS																	
Troglodytidae																	
Catherpes mexicanus	Canyon Wren					5			2		1			3	25	8	0
Salpinctes obsoletus	Rock Wren	2	15	51	32	28	7			10		2		8	67	147	0
Tyrannidae																	
Empidonax spp.	Flycatchers								1					1	8	1	0
Mimidae																	
Oreoscoptes montanus	Sage Thrasher				2	2								2	17	4	0
Picidae																	
Colaptes auratus	Northern Flicker			4										1	8	4	0
Passerellidae																	
Junco hyemalis	Dark-eyed Junco			1			1							2	17	2	0
Pipilo chlorurus	Green-tailed Towhee		1	5										2	17	6	0
Passeroidea																	
Carpodacus spp.	Finches	1												1	8	1	0
Odontophoridae																	
Oreortyx pictus	Mountain Quail		1	3							1			3	25	5	0
Phasianidae																	
Alectoris chukar	Chukar			1										1	8	1	0
TOTAL BIRD EVENTS														10	83	179	0

[a] When both were present, the 2 chipmunk species could be distinguished in some but not all photos, so data were combined.

[b] When both were present, the 2 mouse species could be distinguished in some but not all photos, so data were combined.

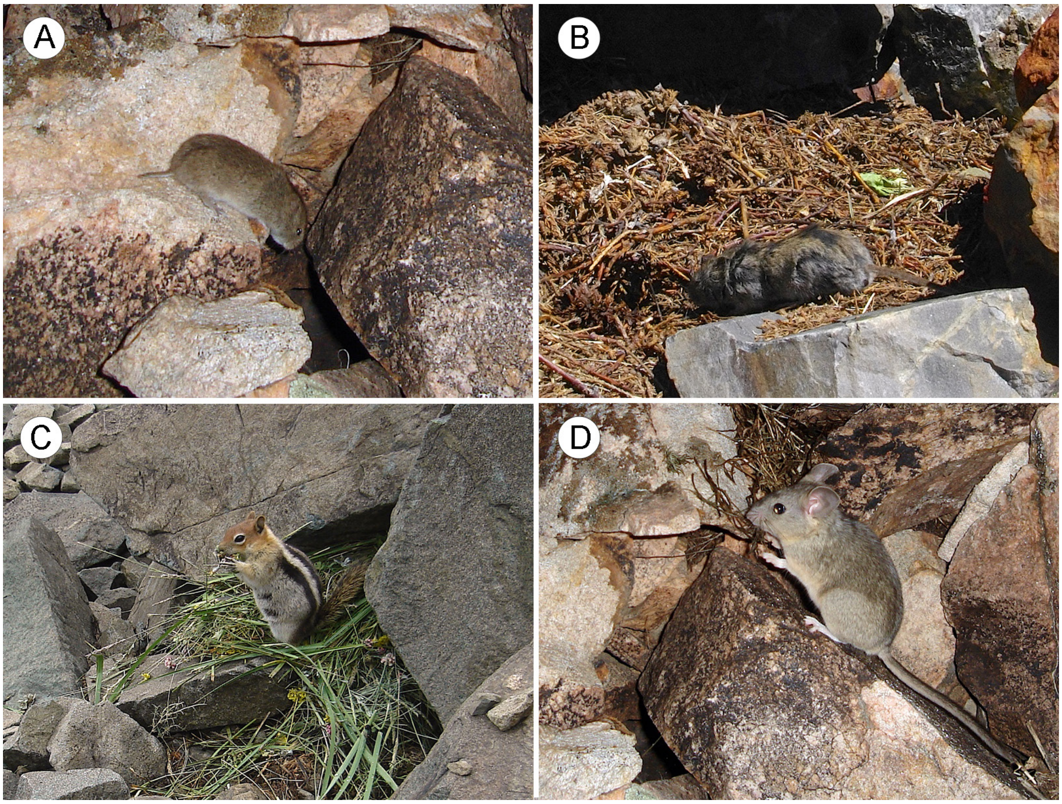

Fig. 5. Small mammal visitors (sympatric herbivores) to American pika haypiles. ***A,*** Sagebrush vole (*Lemmiscus curtatus*). ***B,*** Mountain pocket gopher (*Thomomys monticola*). ***C,*** Golden-mantled ground squirrel (*Callospermophilus lateralis*). ***D,*** Desert woodrat (*Neotoma lepida*).

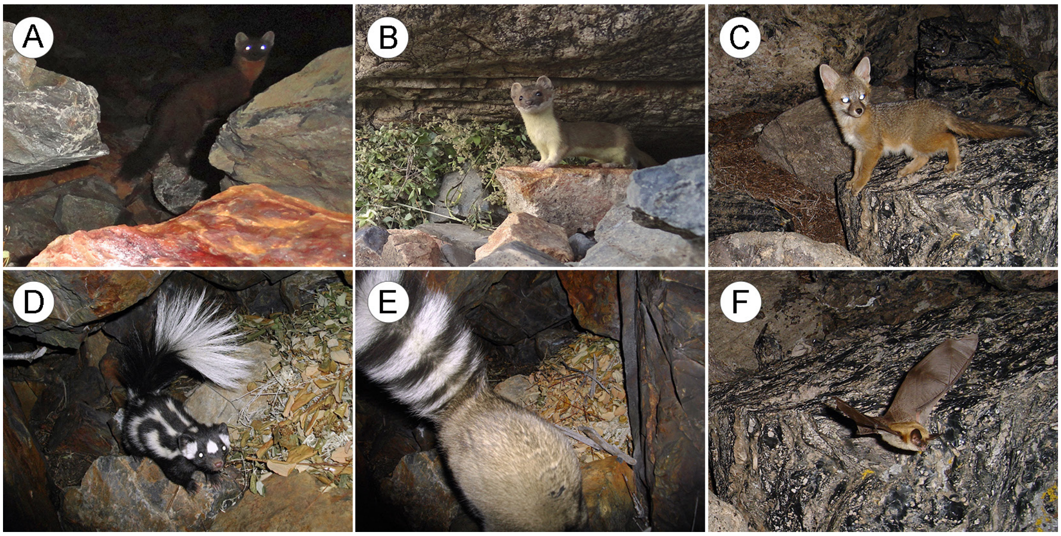

Fig. 6. Mesocarnivores (predators on pikas) and bats at American pika haypiles. ***A,*** Pine marten (*Martes americana*). ***B,*** Long-tailed weasel (*Mustela frenata*). ***C,*** Gray fox (pup; *Urocyon cinereoargenteus*). ***D,*** Spotted skunk (*Spilogale gracilis*). ***E,*** Ringtail (*Bassariscus astutus*). ***F,*** Long-eared bat (*Myotis evotis*).

in the Mono Craters (Table 3, Fig. 6). This species record may have been the result of a moth bloom near the haypile, as moths can be seen in some photos, and long-eared bats and canyon mice appear to be chasing them. Considering known predators of pikas (all Carnivora species in our sample except black bears), long-tailed weasels accounted for the largest number of events (39%; Fig. 6). The long-tailed weasels, together with spotted skunks (23%) and short-tailed weasels (19%), composed 81% of all predator species events.

Birds were photographed at 10 sites including each mountain region, and the photographs represented 10 species from 8 families (Table 3). Rock Wren (*Salpinctes obsoletus*) was overwhelmingly the most commonly photographed species, occurring at 67% of sites and represented by 147 events (82% of the total bird events); other bird species ranged from 1 to 8 events. Most birds photographed were ground dwellers or species that commonly use ground environments. Less expected in talus environments were Northern Flicker (*Colaptes auratus*), captured in 4 events (WMM) in the Bodie Mountains, and a single flycatcher (*Empidonax* sp.), photographed in the Sierra Nevada (VRC).

Diel Activity

Most of the animals we recorded were either 100% diurnal (9 of 26 mammal species) or 100% nocturnal (10 of 26 mammal species; Tables 3, 4). The strictly diurnal species included ground squirrels and tree squirrels, chipmunks, pocket gopher, and black bear (the latter 2 had only one photo event each). The strictly (or nearly) nocturnal species included the mice, voles, woodrats, pine marten, skunk, and ringtail.

Pikas, traditionally considered to have crepuscular behavior, had mixed times of daily activity in our records. Of 4331 total pika events, 58% were diurnal, 27% crepuscular, and 15% nocturnal (Table 4). Activity in the 3 diel periods was recorded at all sites where pikas were present in photos, with distribution varying across sites (Fig. 7). On average, across all 38 periods, the greatest nocturnal activity was recorded at VRC (34%) and the least at BJB (5%), with a period high of 70% at VRC and a period low of 0% at LUN. Diurnal activity ranged from 32% to 66%. The southern Mono Craters site, PUM, had the highest frequency of crepuscular events (50%). Nocturnal events were documented in all seasons of our sampling periods and ranged in representation across sampling periods at the various sites (Table 4).

Of 122 pika predator events, 45% were nocturnal (Tables 3, 4). However, nocturnal activity varied by species, ranging from 0% to 100%, with some site data likely skewed by the low number of recorded events. Notably for the weasels, which are some of the most common pika predators and are traditionally considered active both day and night (Sheffield and Thomas 1997), the short-tailed weasel was photographed at night in 30% of the events, while the long-tailed weasel appeared at night in only 6% of the events.

For sympatric herbivores as a group (mountain cottontail [*Sylvilagus nuttallii*] and all Rodentia), of 1471 total events, 48% were nocturnal, with most species being either strictly nocturnal or diurnal. Important potential competitors, including woodrats and ground squirrels, had contrasting behavior: woodrats were nearly 100% nocturnal (2 diurnal events of 250 total), whereas ground squirrels were 100% diurnal. Overall, predator and sympatric herbivore pressures on pikas appeared to be constant across the 24-h period, at least during the warm season when all species were active.

Talus Temperatures and Relationship of Pika Behavior to Temperature

Mean annual daily temperatures for all positions (talus surface at haypile and talus matrix) and sites ranged from 1.7 °C to 8.8 °C and averaged 5.4 °C (Table 5, Supplementary Material 2). Surface positions were consistently warmer than positions in the talus matrices, and annual mean temperature differences between positions was greatest at the 2 Mono Craters sites (mean talus surface 7.9 °C vs. matrix 2.0 °C). Considering seasonal temperatures, summer talus surfaces were warmer than matrices, with larger means, ranges, and variances of temperatures (Table 5). During the warmest part of the day, mean surface temperatures (25.0 °C) were 10.4 °C warmer than matrix temperatures (14.6 °C), and surfaces had greater amplitude of temperatures than matrices (standard deviation for talus surfaces 4.9 °C vs. matrices 3.2 °C). Nighttime summer mean surface temperatures (14.8 °C) were only slightly warmer than matrix temperatures (14.0 °C). Compared to the other

Table 4. Diel activity of American pikas, predators of pikas, and sympatric small herbivores by site. Crepuscular = 18:00 to 21:00 and 05:00 to 08:00; Diurnal = 08:00 to 18:00; Nocturnal = 21:00 to 05:00. For pikas, overall percent nocturnal activity is given, as well as minimum and maximum percentages recorded at sites with multiple sampling periods.

	Site												
	SER	EMM	WMM	RWB	BJB	STR	VRM	VRC	LUN	NMC1	NMC2	PUM	All Sites
All species													
Events	34	69	338	200	2176	171	893	708	1154	233	42	114	6132
Sample days	32	123	235	96	144	45	42	171	368	64	44	145	1509
Events/day	1.1	0.6	1.4	2.1	15.1	3.8	21.3	4.1	3.1	3.6	1.0	0.8	4.1
American pika													
Events	0	0	139	0	1772	133	849	567	846	3	0	22	4331
Events/day	0	0	0.6	0	12.3	3.0	20.2	3.3	2.3	0.1	0	0.2	2.9
Crepuscular (%)	0	0	27	0	35	26	23	20	22	33	0	50	27
Diurnal (%)	0	0	65	0	61	52	66	46	53	67	0	32	58
Nocturnal, overall (%)	0	0	8	0	5	22	11	34	25	0	0	18	15
Nocturnal, min period (%)		3		3				20	0			0	5
Nocturnal, max period (%)		19		8				70	55			23	35
Predators[a]													
Events	1	3	22	25	19	1	2	6	32	6	2	3	122
Events/day	0.03	0.02	0.09	0.26	0.13	0.02	0.05	0.04	0.10	0.09	0.05	0.02	0.1
Nocturnal (%)	100	33	55	48	16	0	0	17	50	83	100	33	45
Sympatric herbivores[b]													
Events	30	49	112	140	350	29	42	131	266	194	38	89	1470
Events/day	0.9	0.4	0.5	1.5	2.4	0.6	1.0	0.8	0.7	3.0	0.9	0.6	1.0
Nocturnal (%)	83	47	38	49	40	0	19	38	79	39	84	65	48

[a] Predators include gray fox, bobcat, pine marten, short-tailed weasel, long-tailed weasel, spotted skunk, and ringtail.

[b] Sympatric herbivores include mountain cottontail, yellow-bellied marmot, golden-mantled ground squirrel, California ground squirrel, Belding's ground squirrel, Douglas's squirrel, least chipmunk, lodgepole chipmunk, Great Basin pocket-mouse, sagebrush vole, long-tailed vole, bushy-tailed woodrat, desert woodrat, deer mouse, and canyon mouse (see Table 3 for scientific binomial species names).

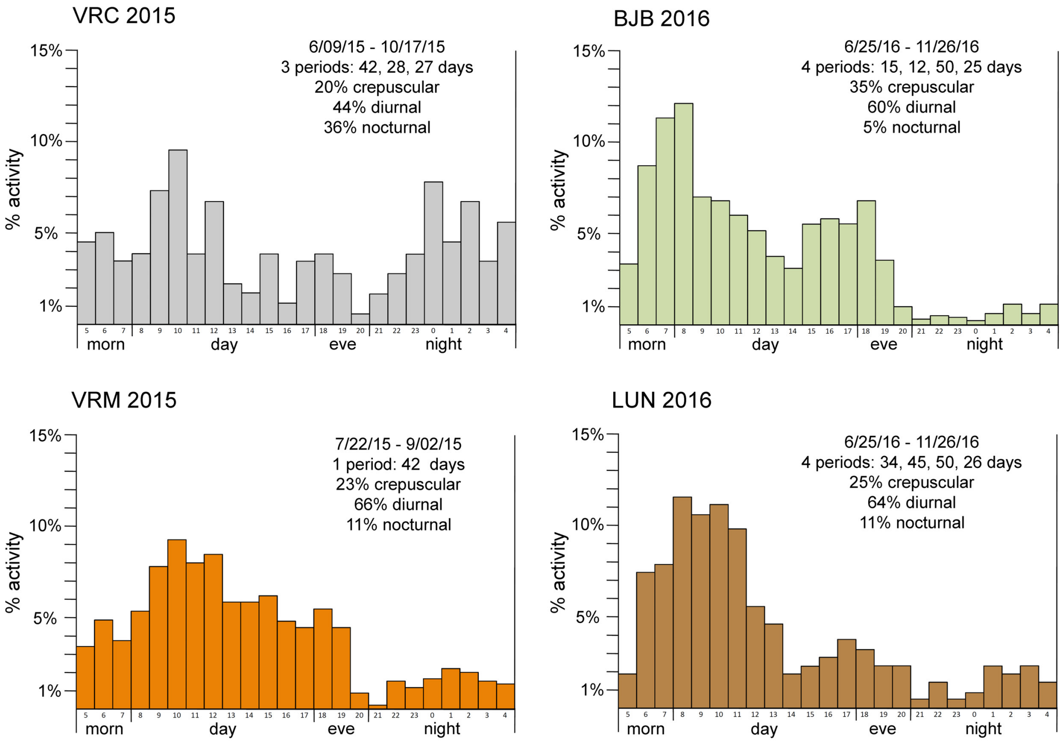

Fig. 7. Variation in American pika diel activity by site and year. See Table 1 for site names. Date format is mm/dd/yy.

mountain ranges, the Mono Craters sites had consistently colder summer matrix temperatures and lower amplitudes relative to surface temperatures for all times of the day (Table 5).

In winter, time of day had little effect on talus temperatures, such that day and night patterns were generally similar for surfaces and matrices, and trends followed the overall mean daily pattern (Table 5). Lack of a diel temperature effect likely resulted from snow covering the sites, which would insulate surfaces and matrices and minimize the influence of outside air temperatures. The primary winter mountain range effect was colder matrix than surface temperatures at all times of the day at Mono Craters, whereas at the other sites, the opposite mostly occurred.

To evaluate the relationship between daytime temperatures and nocturnal pika events, we calculated relative temperatures by sites and calendar periods that included observed nocturnal events within a sampling period (Table 6). Overall, mean temperatures at haypile surfaces for the warmest part of the day before pika nocturnal events were cooler than the mean daily maximum temperature for the reference period, except during winter sampling periods (Fig. 8). Variances were high, however, and differences were not significant ($P > 0.05$). Middays before observed nocturnal events were far cooler than the daily maximum temperatures for the warmest 10% of the days in the reference period (Table 6). There was no evidence that excess summer daytime heat events were related to increased night activity at haypiles. Mean night temperatures for the dates of summer nocturnal activity were consistently warmer than mean daily minimum temperature for the reference period, but variances again were high and the differences were not significant ($P > 0.05$).

Diel behavior during the cold season suggested a different pattern from summer, although we had only 3 intervals for comparison. For 2 of these intervals (Table 6, Fig. 8: BJB-2, LUN-2), mean temperatures of the day before the nocturnal events were warmer than the mean maximum daily temperature of the reference period. For the third cold-season interval (LUN-4), the pattern was similar to that of summer.

TABLE 5. Summary of mean temperatures and standard deviations (SD) from data loggers at American pika sites where trail cameras were set. Temperatures are given for the talus surface at the haypile and the talus matrix (~0.75 m in talus subsurface). Summer = 15 June–15 September; Winter = December 15–March 15. Summer night = 20:00, 24:00, 04:00; Summer morning = 08:00; Summer afternoon = 16:00; Winter night = 16:00, 20:00, 24:00, 04:00, 08:00; Winter day = 12:00. Surf. = Surface, Mx. = Matrix.

Annual temperatures (°C)

	Daily		SD	
Mtn. range	Surface	Matrix	Surface	Matrix
Bodie Mtns.	6.2	5.0	10.1	8.8
Sierra Nevada	5.8	5.5	9.1	7.9
Mono Craters	7.9	2.0	10.1	6.1
MEAN	6.3	4.6	9.6	7.4

Summer temperatures (°C)

	Daily		SD		Night		SD		Morning		SD		Noon		SD		Afternoon		SD	
Mtn. range	Surf.	Mx.	Surf.	Mx.	Surf.	Mx.	Surf.	Mx.	Surf.	Mx.	Surf.	Mx.	Surf.	Mx.	Surf.	Mx.	Surf.	Mx.	Surf.	Mx.
Bodie Mtns.	17.9	15.7	6.2	3.2	15.4	15.7	4.5	3.1	14.1	13.6	3.1	2.5	22.7	15.5	3.5	2.6	25.0	18.1	4.6	3.0
Sierra Nevada	18.3	16.1	6.2	5.1	15.4	15.9	3.9	4.1	16.0	13.6	4.0	3.4	24.4	16.9	6.3	4.3	22.2	18.8	4.6	4.2
Mono Craters	19.0	6.8	8.2	1.2	12.4	6.7	4.2	1.0	15.1	6.5	3.5	1.1	31.2	7.3	4.1	1.5	23.2	7.4	3.4	1.3
MEAN	18.3	14.2	6.6	3.8	14.8	14.0	4.0	3.2	16.5	12.2	3.6	2.7	25.0	14.6	4.9	3.2	23.4	16.3	4.4	3.3

Winter temperatures (°C)

	Daily		SD		Night		SD		Day		SD	
Mtn. range	Surface	Matrix	Surface	Matrix	Surface	Matrix	Surface	Matrix	Surface	Matrix	Surface	Matrix
Bodie Mtns.	−3.6	−3.2	3.3	1.3	−3.7	−3.2	3.1	1.4	−2.7	−3.3	3.7	1.4
Sierra Nevada	−1.5	−1.3	2.4	2.3	−1.5	−1.3	2.4	2.3	−1.3	−1.4	2.6	2.3
Mono Craters	−2.3	−3.8	3.7	4.0	−2.6	−4.0	3.8	4.1	−0.8	−3.5	5.2	3.8
MEAN	−2.3	−2.3	2.9	2.5	−2.4	−2.3	2.9	2.5	−1.6	−2.3	3.5	2.4

TABLE 6. Mean temperatures with standard deviations (SD) during pika nocturnal event periods compared to reference periods. Reference periods extend ~7 d before the first nocturnal event and extend ~7 d after the last nocturnal event. Tmax = maximum daily temperature, Tmin = minimum daily temperature. For nocturnal events, data are given for mean Tmax of the day before the event and the mean temperature of the night of the event. All temperatures were measured at haypile surface positions.

			Reference period mean daily temp (°C)							Nocturnal event mean temp (°C)			
			Daily		Tmax		Tmax 10% warmest days	Tmin		Tmax day before		Night of event	
Site (interval)	Reference temperature period	Nocturnal events nights	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
WMM	1 Jul 2018–1 Sep 2018	5, 5	17.5	4.5	22.6	4.0	28.5	14.0	2.8	20.2	3.7	15.2	4.3
STR	15 Jul 2016–15 Sep 2016	29, 17	18.7	6.4	29.0	4.8	33.0	13.9	2.9	25.3	4.4	16.7	1.8
BJB-a	30 Jul 2016–30 Sep 2016	28, 14	15.3	5.7	19.4	4.8	26.8	11.3	4.0	19.2	6.4	14.0	5.7
BJB-b	1 Oct 2016–1 Dec 2016	19, 14	0.8	4.4	2.7	5.0	11.5	−0.4	3.9	3.1	5.7	1.2	4.0
VRM	10 Jul 2015–10 Sep 2015	97, 35	16.8	3.7	20.6	2.9	24.1	14.1	2.4	19.2	2.5	17.3	2.3
VRC-a	15 Sep 2014–15 Nov 2014	60, 18	8.9	7.0	14.6	6.5	24.7	4.9	4.5	13.1	5.8	7.0	4.2
VRC-b	1 Jul 2015–1 Nov 2015	71, 36	16.7	5.2	19.0	3.4	26.2	15.3	4.7	17.8	4.1	17.7	4.0
VRC-c	15 Jul 2016–15 Oct 2016	63, 25	15.4	9.6	28.8	6.3	34.9	8.5	4.1	21.7	8.3	8.7	5.6
LUN-a	10 Jul 2015–10 Nov 2015	49, 24	15.6	6.7	17.8	6.9	26.2	14.2	6.2	17.0	5.2	16.6	5.5
LUN-b	15 Nov 2015–15 Feb 2016	54, 33	−1.9	3.5	−1.3	3.6	6.5	−2.2	3.4	−1.2	3.9	−1.8	3.5
LUN-c	15 Jun 2016–15 Aug 2016	17, 14	21.9	4.4	26.4	3.1	30.4	18.6	3.4	24.3	1.6	21.5	1.9
LUN-d	20 Sep 2016–20 Apr 2017	61, 43	2.3	5.4	3.3	6.4	17.6	1.7	4.7	2.8	6.9	2.2	6.3
LUN-e	1 Jun 2017–1 Nov 2017	13, 23	13.9	7.8	17.8	8.3	30.0	11.4	6.5	17.8	9.9	14.3	8.8

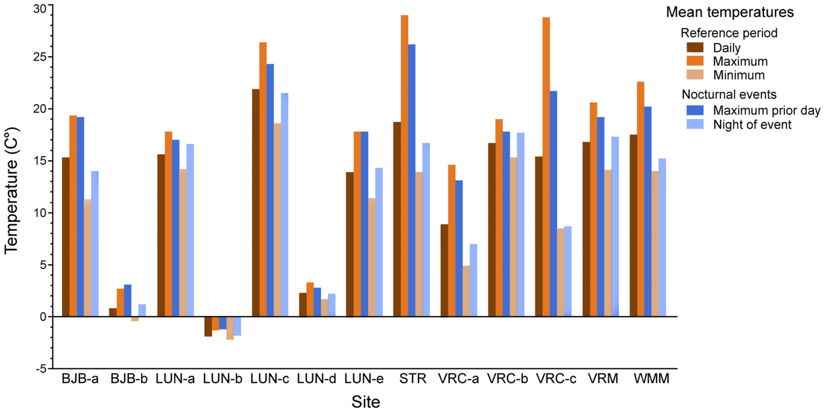

Fig. 8. American pika nocturnal events and reference period temperatures. Mean nighttime temperature of days with nocturnal events (Night of event) and mean temperature of the midday before the nocturnal event (Maximum prior day), compared to mean daily temperature (Daily), mean maximum daily temperature (Maximum), and mean minimum temperature (Minimum) of reference periods. See Table 1 for site names.

Additional Pika Observations

In addition to patterns of animal activity described above, camera traps provided insight into pika behaviors that have been characterized in the literature (Smith and Weston 1990), as well as some that, to our knowledge, have not been previously documented. While most of our 38 sampling periods were during the warm season (early summer to early fall), we collected data from 9 cold-season periods (late September to late March) at LUN, VRC, and BJB, including times when haypiles were under snow. Many behaviors recorded in summer were also recorded in winter, with foraging being the main activity that was absent. Pika-related behaviors we documented include the following (Figs. 9–13): foraging, haying, tending haypiles, eating foraged plants, eating pieces of snow, licking icicles, using latrines, eating fecal pellets, carrying caecotrophs and marmot scats, juveniles visiting occupied haypiles, territorialism, chasing, changing haypile residency, kleptoparasitism, sleeping on haypile, napping in snow, vocalizing, vigilance, visiting inactive haypiles, cheekrubbing, and scent-marking. We describe specific behaviors and observations below.

PIKA CO-OCCURRENCE/KLEPTOPARASITISM.—Of 4331 total pika events and 10,336 photos, the vast majority (99.9%) included only one pika per photograph. The exception was at BJB, where several sequences of photos showed 2 pikas together at one haypile (Fig. 13). These photos occurred on 22–25 November 2016 and documented a nonresident pika (not seen before at the haypile) repeatedly entering the scene and taking vegetation from the haypile (kleptoparasitism). The resident pika did not appear to chase the intruder in the sequences captured, which we interpret as social tolerance, perhaps by a resident female to an adjoining territorial male. Before and during the dates of this incident, considerable snowpack had developed over the haypile. Prior to intrusion by the nonresident pika, the resident was regularly photographed at and near the haypile, eating plants and snow and tending the haypile.

PREDATION EVENTS.—Of 125 photos showing predators of pikas at haypiles, no predation events on pikas were recorded. A single haypile turnover incident, described below, may be indirect evidence that predation resulted in a temporary vacancy. And one photo showed both a pika atop its haypile and a long-tailed weasel below the haypile (Fig. 14); in the subsequent photos, the pika disappeared and the weasel moved around within the frame of the camera.

TERRITORIAL BEHAVIOR AND RESIDENCY TURNOVER.—In a series of photographs over 16 d in October 2014 at VRC in the Sierra Nevada, we recorded territorial behavior and an apparent turnover in haypile residency (Fig. 12). An adult pika (pika1), bearing notches on both ears, had been photographed regularly at this site and was assumed to be the haypile resident.

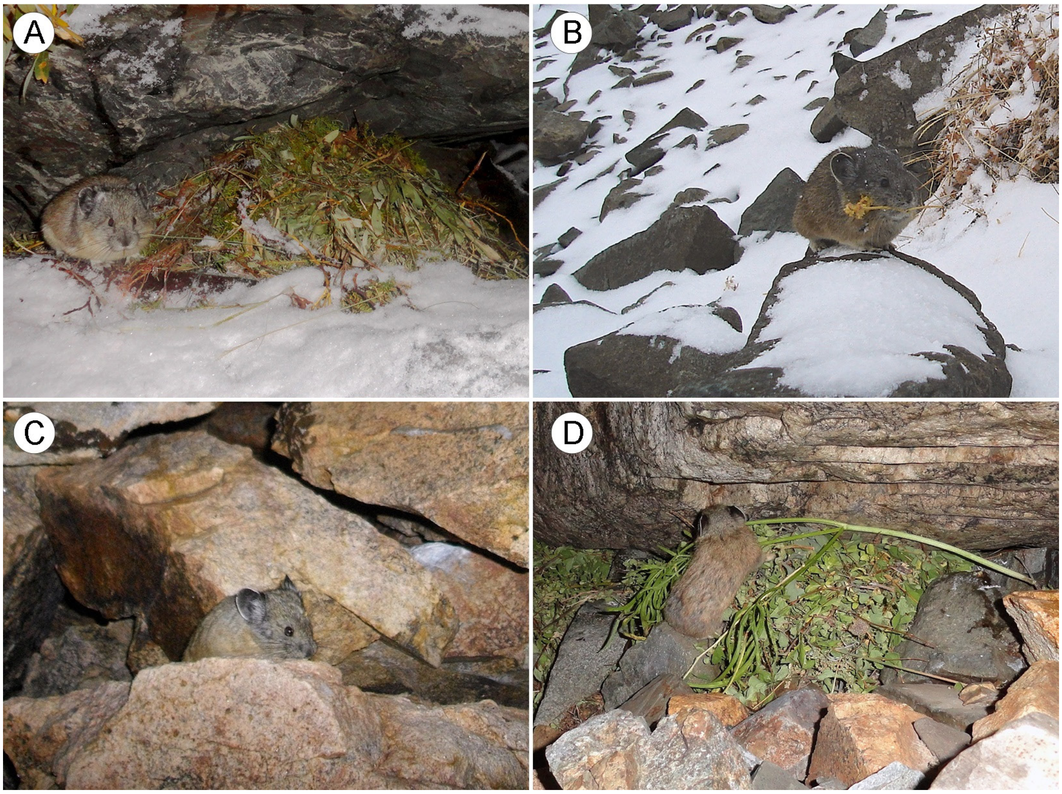

Fig. 9. Night and winter activity by American pikas. ***A,*** Night at winter haypile. ***B,*** Winter day on rock outside haypile. ***C,*** Night movements. ***D,*** Night foraging.

A second pika (pika2), a juvenile without ear marks, was photographed at the haypile in 2 sequences, where it appeared in 2 photos at 03:45 on 6 October and in 1 photo at 02:03 on 9 October. The latter visit was followed 36 s later by a photo of pika1 at the same spot on the talus where pika2 had just been, suggesting it had chased off pika2. Then, at 02:04, pika1 was photographed sitting on the haypile and was thereafter photographed several times sleeping on the haypile for the rest of the night, which we interpret as further territorial behavior. Pika2 was not photographed over the next 13 d, but pika1 was present in more than 100 photos throughout this period. The last photograph of pika1 was taken at 10:24 on 22 October; the cause of pika1's disappearance is unknown. Four hours later, at 14:04, pika2 ran through the haypile environment, and a similar event occurred at 18:15. The following morning (23 October, 09:47), pika2 was photographed sitting on pika1's common perch rock, followed 7 s later by pika2 eating a leaf near the haypile. Then, at 10:08, pika2 was photographed roosting on the haypile. Pika1 was never seen again, and pika2 was photographed frequently from that day until the camera batteries died 13 d later on 4 November.

NIGHT AND COLD-SEASON FORAGING.—One set of photos across 24 h at VRC captured nighttime foraging by a resident pika after a snowstorm. At 21:56 on 27 September 2014, the pika returned to its snow-surrounded haypile carrying a branch of Brewer's mountain heather (*Phyllodoce breweri*). Temperatures recorded by the datalogger at the haypile were 1.0 °C at 20:00 and 0.5 °C at 24:00. Over the next 24 h, the pika was photographed 12 times sitting at and eating from the haypile. Temperatures remained between 0.5 °C and 1.0 °C until 16:00 on 28 September, when they rose to 3.0 °C and snow began melting from the haypile area. In other night and cold-season foraging events, pikas were photographed carrying branches of *Angelica,*

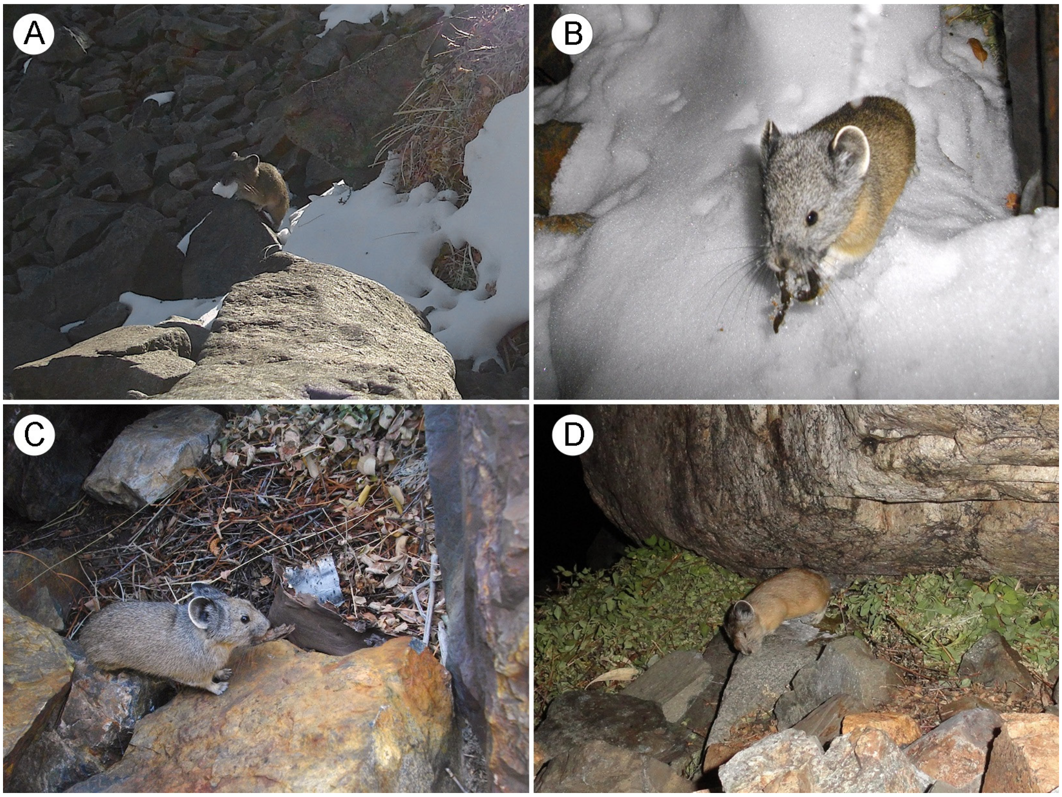

Fig. 10. Diverse American pika behaviors photographed at camera trap haypile sites. ***A,*** Carrying snow. ***B,*** Carrying caecotrophs. ***C,*** Carrying stick. ***D,*** Juvenile cheek-rubbing.

Symphoricarpos, Holodiscus, Eriogonum, and *Veratrum* (Fig. 9), as well as sticks and pieces of dry wood at LUN and VRC and a marmot scat at BJB at 21:40. However, although our photographs from haypile sites during active foraging suggest that nocturnal foraging occurs, it is rare, and tending and organizing the days' growing haypile are the more common additional nocturnal activities during the haying season.

Time to detection.—For pika sites known to be occupied, and where haypiles contained fresh vegetation, the average time from camera deployment to the first pika photographed was <24 h. During some years at some of these sites, haypiles did not contain fresh vegetation ("inactive haypiles"); the average time to first pika detection in these situations was 19 d. For sites presumed to be extirpated, but where cameras documented pikas, the average time to first pika detection was 35 d. In particular, time to first detection was 51 d at WMM, and 40 d at NMC1.

Discussion

Potential Biases of Camera Traps

Despite camouflage and hidden placement of trail cameras, animals are known to detect and react to camera activity in their habitats (Gibeau and McTavish 2009, Meek et al. 2016, Rovero and Zimmerman 2016). Camera presence has been shown to affect behavior in many species, deterring as well as attracting visits and affecting natural movements. Effects are inconsistent within species, although some species have greater awareness of cameras during days or more startle responses at night (Meek et al. 2016). Intrusive effects from cameras, summarized by Meek et al. (2016) as "too noticeable … in a way that is disturbing or annoying," seem to occur more often in large predator species than in small herbivore species (De Bondi et al. 2010, Hamel et al. 2013, Trolliet et al. 2014). Midsize and small predators, such as weasels and feral cats, react to both white flash and infrared cameras, and white

Fig. 11. American pika haying behavior. ***A,*** Early haying. ***B,*** One-month later.

flash is more likely to frighten small mammals (Bengsen et al. 2011, Glen et al. 2013). Much of this research, however, addresses irregular visitations by ranging species. It does not address situations in which cameras target resident species that are anchored to a home place (e.g., haypile, burrow, stickhouse) and will quickly habituate.

Despite concerns about cameras causing behavioral disruptions, negative effects are likely far less than would be expected if a researcher were present and directly observing behavior (Bridges and Noss 2011). In addition, compared to live-trapping, cameras are equally effective for presence-absence mammal detections, as well as more cost effective (DeBondi et al. 2010, McDonald et al. 2010) and far less disruptive. For exploratory and descriptive studies such as ours, cameras have allowed continuous 24-h monitoring of pika haypiles as well as detection of a broad suite of nontarget species. Pikas are known to react when human observers enter their territories, but they readily habituate and resume activity despite continuing human presence (Smith and Ivins 1984, Stafl and O'Connor 2015). Indirect evidence that our cameras were not frightening pikas from haypiles or significantly deterring them from natural behavior came from the large number of pika photos at our active sites, both during the day (without flash) and at night (with flash). Further, our cameras documented a range of behaviors previously described for pikas from field observations (Smith and Ivins 1984), as well as new behaviors, suggesting tolerance. Our images detected no obvious sequences that could be interpreted as pikas showing fear of the camera,

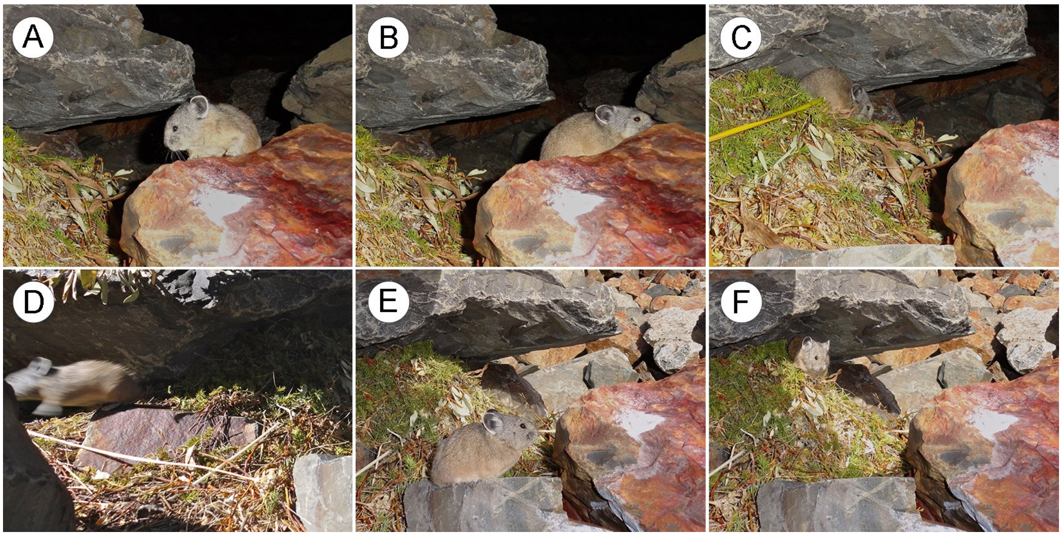

Fig. 12. American pika territorialism. Haypile defense (A–C) and turnover (D–F). ***A,*** Pika2 (juvenile) visiting haypile on 9 October at 02:03. ***B,*** Pika1 (resident) at same spot 36 s later. ***C,*** Pika2 sleeping on haypile for remainder of night. ***D,*** Pika2 checking haypile on 22 October, 4 h after final photo of pika1 was recorded. ***E,*** Pika2 eating from haypile the next morning at 10:08. ***F,*** Pika2 takes over haypile for remainder of sampling period. See text for further details.

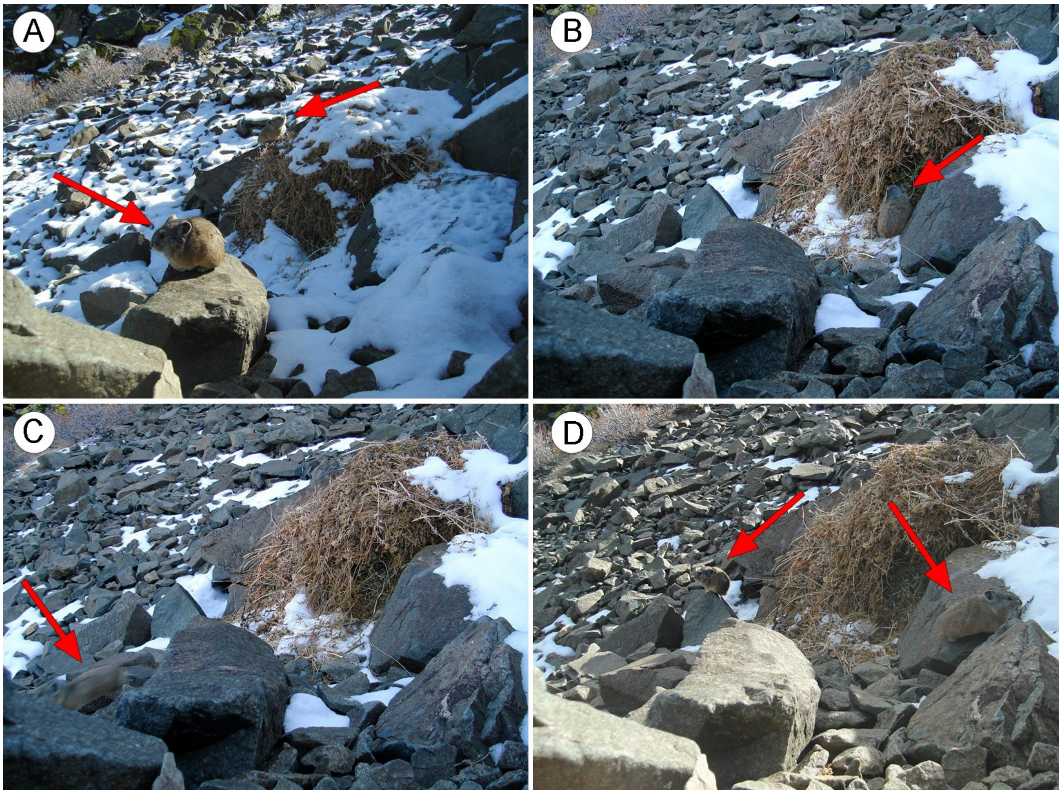

Fig. 13. Two-pika sequence. ***A,*** Resident and visitor American pikas together without obvious aggression. ***B,*** Visitor takes vegetation. ***C,*** Visitor dashes away. ***D,*** Resident perches, visitor returns.

Fig. 14. American pika and long-tailed weasel co-occurrence with seeming lack of mutual awareness. In subsequent photos, the pika was absent and the weasel continued to inspect the haypile. Arrows point to pika (above) and weasel (below).

suggesting that pikas were not inhibited by being photographed. Similar camera explorations of small herbivore behavior have been conducted for many species without encountering camera bias, such as for the extremely rare Australian central rock-rat (*Zyzomys pedunculatus*; McDonald et al. 2010) and the endangered Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*; Edelman et al. 2005) as well as for the American pika (Hall and Calfoun 2019, Camp et al. 2020) and the elusive Ili pika (*Ochotona iliensis*; Li and Smith 2015). While acknowledging potential undesired effects of cameras on detectability and behavior, we conclude that camera-related disturbances do not seriously distort the interpretations we present.

Beyond these issues, a potential bias in our study relates to the positioning of our cameras, in that we deployed only one camera per site and all cameras were directed at haypiles (discussed also by Massing 2012 and Camp et al. 2020). The camera traps were also set at a low height and at short distances from the haypile, which confined the scene and may bias our records toward small animals. Without observations elsewhere on or off the talus we cannot conclude that the activities we documented, such as diel behavior, accurately represent times pikas spent within or beyond the talus other than at the haypile position. This bias might be especially significant for marginal sites such as most of ours, where scatter-hoarding is more common than central-place behavior, or in places where caching activity is less frequent than at more typical sites (Smith et al. 2016, Varner et al. 2016). Furthermore, observations of other mammal species captured by our cameras can only be interpreted to represent animals that visited pika haypiles and could fit within the confined scene or be caught in the photo background. Thus, these images may depict activity that differs from activity in the talus more generally. However, many photos documented behaviors that suggested the non-pika species were present specifically to take the haypile contents (raiders) or to hunt the pika or other occupants (predators). Recognizing these biases, we restrict interpretations of our photographs and data accordingly.

Detection of Pika Occupancy

Cameras deployed at 12 pika sites corroborated field observations of active occupancy and provided important evidence about uncertain occupancy and presumed extirpated sites. At sites of known pika occupancy and high activity, such as VRC, BJB, VRM, and LUN, cameras captured hundreds to thousands of photos of pikas per site. At these locations, pikas exhibited a range of behaviors and were active day and night throughout the year, demonstrating the value of camera traps for verifying occupancy and documenting behaviors.

Arguably the most important finding from our study was that cameras documented pika occupation at 2 sites where pikas were presumed to be extirpated, WMM and NMC1. In the former case, 51 d after the camera was installed, 139 photos of pikas were captured, depicting a range of activities, including haying, foraging, and surveillance, suggesting new residency. Our conclusion—that these images depicted a resident pika rather than a transient one—was corroborated after the cameras were removed when, in the field, we observed pika vocalizations and continued addition of fresh vegetation to the haypile. Documenting occupancy at the WMM site is particularly important for the assessment of pika status at the mountain range scale. In the Bodie Mountains, which, under current climates, are biogeographically isolated from mainland ranges containing abundant pikas (Millar et al. 2014a), patch and metapopulation declines and extirpation have been occurring rapidly in recent decades (Millar et al. 2013, 2014a, Smith and Nagy 2015, Nichols et al. 2016). Less than a century ago, pikas were documented as abundant in the southern end of the range in native and anthropogenic habitats around the historic mining town of Bodie (Severaid 1955) and in anthropogenic habitats at scattered mining town locations in the central and north end of the range (Smith 1974). From indirect sign, pikas appear to have been widely distributed throughout the range wherever rocky habitat occurs (Millar et al. 2014a; Millar personal observations).

By the early 21st century, beyond the anthropogenic ore dumps at Bodie, pikas were known to persist in only 5 locations in the range: a roadcut-talus in the western side of the range along SR 270 and at 4 sites in the north end of the range (Chemung Mine and Serita Mine [both ore dump habitats] and East Masonic Mountain and West Masonic Mountain [both native habitats]; Millar et al. 2013). We deployed cameras at the last known remaining occupied sites in that region, having last documented occupancy from field surveys at Serita Mine and East Masonic Mountain in April 2012 and at West Masonic Mountain in July 2015, when green haypiles were scattered throughout the taluses at all sites. At WMM, no further definitive direct or indirect signs were observed until our cameras documented pikas there in early summer 2017. We continued to photograph pikas in all sampling periods until the camera was removed in autumn 2019. Visible field signs of pika occupancy, however, were not observed until August 2019, when images first showed fresh vegetation in the haypile.

The value of cameras for documenting pikas at assumed extirpated locations was further shown at the Mono Craters. This small mountain range—composed of overlapping eruptive volcanic cones, surfaced by recent rhyolitic pumice, and supportive of sparse vegetation—is an unlikely environment for pikas. Smith et al. (2016) documented active use on talus slopes in the south end of the range where our PUM site (2558 m) was stationed. Smith et al. (2016) characterized behaviors at this extreme marginal site that were different from those at more typical pika habitats, including more scatter-hoarding, fewer central-placed haypiles, and less surface activity. Our cameras corroborated pika visits to the only obvious haypile at that site (PUM), albeit at a very low level of activity—just 22 events in 145 d of sampling.

Beyond the south end of the Mono Craters, pika occupancy had been observed at several sites in the central part of the range (Millar et al. 2018), and pika vocalizations and one green haypile were observed at the north end of the range in 2013. We observed no subsequent field sign of definitive occupancy in that part of the range. We first deployed cameras in the north Mono Craters in 2018 at a location 2 km from the 2013 occupied site, at a considerably lower elevation than PUM, and in a talus where haypile vegetation appeared to be only a few years old (NMC1 and NMC2; 2218 m).

At NMC1, we photographed a pika 3 times in 64 d of sampling. Fresh vegetation did not appear in the haypile, and field observations during or after the camera sampling periods were not successful in documenting pikas anywhere in the north Mono Craters region. In contrast to the situation at WMM, camera evidence of pikas at NMC1 suggests a transient visit by a single juvenile pika who came from an unknown local territory or was in the process of dispersing from another talus area in the Mono Craters. Regardless of where this pika came from, given the isolated nature of the north Mono Craters, the photos of pikas indicate that the species can persist in such marginal sites without being visible to field observation for as long as 6 years.

In addition to documenting pika presence in sites assumed to be extirpated, cameras corroborated field assessments of apparent extirpation at other locations. As noted above, several north Bodie Mountain locations were active until 2012. Despite annual field surveys in summer and fall over the following years, no signs of occupancy were observed in the vicinity of the SER or EMM sites. In spring 2017, we explored a new area of pika use, Red Wash Butte, which is a very small, isolated talus 2.5 km east of the EMM site. There we found abundant fresh-appearing perched pellets and numerous haypiles with vegetation appearing <2 years old at the time. However, cameras at all 3 of these sites (SER, EMM, RWB) failed to record pikas during 32 d, 123 d and 96 d of recording, respectively, implicating site extirpation, especially in the areas of the EMM and RWB sites. While lack of evidence is not confirmation of extirpation, especially because we had only one camera per site, these findings give additional insight into the status of pikas at those sites and the sampling effort that may be needed for detection in areas thought to be inactive.

Animal Diversity and Implications for Pikas

To our knowledge, we report the first list of wildlife species at pika haypiles. As a result of the high quality of both the daytime and nighttime images from our custom camera traps, diagnostic markings of animals were readily discernable, enabling species identifications to be made with confidence. We detected 33% of the 78 mammal species known to occur in the greater Mono Basin region as well as 2 species (ringtail and canyon mouse) listed as potentially occurring there (Harris 2017; Supplementary Material 3). Regarding ringtail, however, a first observation for Mono County had been made in February 2016 from a trail camera photograph in the Mono Basin (iNaturalist, accessed 23 April 2020), 9 months prior to our detection. Our record for canyon mouse appears to be the first for Mono County, although it is within the range and habitat given in Jameson and Peeters (2004). While most of the species we photographed are common for the region, several were not expected to use talus habitat, including the following: mountain pocket gopher, desert woodrat, black bear, spotted skunk, bobcat, gray fox, and long-eared bat.

Within a small geographic area in the Bodie Mountains, around the historic townsite of Bodie, California, Smith (1979) recorded 30 mammal species, describing that number as significant diversity for the cold sagebrush steppe environment. Because the Bodie area is more representative of the interior ranges in our study than is the Sierra Nevada–inclined faunal list of Harris (2017), it makes sense that, of our 26 species, 15 overlapped with the Bodie set. Notably, the Smith (1979) record, although encompassing a small area (8 km^2), included 4 distinct habitats, including sagebrush shrub communities, dry and wet meadows, and rock cliffs and talus (including natural and anthropogenic ore dumps). By comparison, our 26 mammal species were recorded from only one habitat type (talus), which is homogeneous in structure and limited in complexity.

The large number of mammal species and frequency of animals documented at haypiles suggest that significant pressure on pikas is exerted from sympatric herbivores as well as from predator species. Potential competitors (i.e., other pikas as well as sympatric small mammals) directly remove vegetation from pika caches (Fig. 5) and might compete for talus residency. Small sympatric herbivores are also likely to indirectly affect forage abundance and availability for pikas in talus forefields. In the low-dry sites of our study, vegetation is routinely sparse. Often, woody shrubs compose the dominant plant communities, increasing competition for adequate nutritive foliage. The nearly balanced distribution of night versus daytime activity of the sympatric herbivores implies a continuous pressure on pikas. Pikas' capacity for activity throughout the 24-h day/night cycle should be advantageous relative to all other sympatric herbivores (except mountain cottontails), which are restricted in daily activity (Holmes 1991). Further, many of the herbivore species that we photographed hibernate in the cold season, and several species estivate in the warm season, removing pressure on pikas during those periods. Of the species we photographed, mountain cottontail, Douglas's squirrel (*Tamiasciurus douglasii*), bushy-tailed woodrat (*Neotoma cinerea*), desert woodrat, deer mouse, and canyon mouse do not hibernate or only hibernate for brief periods. These species could therefore impose persistent pressure on pikas.

Weasels are likely the most important predators of pikas (Ivins and Smith 1983), and they were the most frequent predators in our camera observations (58% of 123 predator species events). Weasels were photographed at 7 of our 8 active pika sites and at 2 unoccupied sites, at night and during the day, although they were more commonly active during the daytime. The second most frequently documented carnivore, the spotted skunk, is likely a minor predator of pikas, given its lesser capacity to descend into the small talus voids that pikas use for retreat. This limitation is similar for martens and other mesocarnivores (Ivins and Smith 1983). Predatory birds are likely to prey on pikas, but we did not photograph any at the haypiles. Because the haypiles were sheltered under boulders and adjacent to tunnels where pikas could safely retreat, it is not surprising that we did not observe direct mammal or bird predation events.

Behavioral studies of pikas based on field observations have documented nontarget species on pika talus, but most sightings have been anecdotal and daytime records. For instance, at a Rocky Mountain location, pika competitor species that were noted during intensive behavioral studies included marmot, chipmunks, tree squirrel, ground squirrels, woodrats, hares, and deer, as well as 2 predator species, namely weasels and marten (Ivins and Smith 1983, Smith and Ivins 1984). At the PUM site, Smith et al. (2016) observed golden-mantled ground squirrels, lodgepole and least chipmunks, and Douglas's tree squirrel running across the talus. They also observed long-tailed weasels crossing the talus and eliciting alarm calls from the resident pikas.

Talus Thermal Conditions and Relationships to Pika Behavior

Prior studies have investigated the thermal conditions of talus inhabited by pikas in several parts of the species' range, including the Great Basin and adjacent regions with similar climates (Beever et al. 2010, Wilkening et al. 2011, Millar et al. 2014b, 2016, Shinderman 2015, Smith et al. 2016, Rodhouse et al. 2017). These and other studies document cool conditions of talus interiors, especially in summer, with attenuated daily extremes relative to the talus surface and outside air temperatures. The talus thermal conditions of our study follow these trends, with consistently cooler temperature in talus matrices than at haypile positions in both summer and winter, and with consistently smaller daily temperature fluctuations within the matrices. We expected haypile positions to be cooler than exposed talus surfaces, as found by Millar et al. (2016), in that haypiles are generally insulated from direct solar radiation by overhanging boulders. The even cooler thermal regime of talus interiors is especially important for pikas, given the low elevation, south aspect, and warm climate found at the majority of our study sites.

The differences between surface and matrix mean daily temperatures were particularly striking at the Mono Craters sites, where the mean difference at the hottest part of the day in summer was 16 °C. A similar finding of cold and stable matrix temperatures has been measured previously at sites in the Mono Craters and Inyo Craters (Millar et al. 2016, Smith et al. 2016), as well as at other lava-flow pika habitats (Shinderman 2015, Ray et al. 2016, Rodhouse et al. 2017).

Mean midday temperatures of talus haypile positions overall were >23 °C (Table 5, Supplementary Material 2), with maximum temperatures reaching 35–45 °C at several sites. Even pikas resting in the shade on the haypiles at those temperatures would likely suffer physiological distress (Smith 1974), implying that continued persistence at these warm sites depends on the ability of pikas to retreat into the cool interior of the talus during the warmth of midday. However, daytime activity captured by our cameras even on the warmest summer days suggests that pikas can endure at least short bursts of surface activity, presumably relying on the cool talus matrices for relief (Smith et al. 2016). Still, given that our cameras only documented activity at haypile positions and not in talus depths, these ideas must be considered speculative.

Similarly, our observations on relationships between nocturnal activity and temperature must be restricted to behavior observed at haypiles and not to the extent of a pika's home range. Observations of pika activity at all hours of the day and night, including in winter, are not surprising, especially considering that the haypile is a pika's primary resting/sentinel place. Notwithstanding, our results did not provide evidence that pika nocturnal activity in the warm season was related to temperature; the hypothesis that pikas would be more active on nights following warm days was not supported. In contrast to summer behavior, our cold-season observations suggested that pikas were more nocturnally active at their haypiles on nights that followed high midday temperatures, as well as during nights that were warmer than mean night temperatures. And while we can only infer night activity by analyzing the nocturnal behaviors documented at the haypile positions, overall our photos suggest that nocturnal foraging and haying are rare, whereas activities that don't require travel from the haypile, such as tending and organizing the days' haying, are more typically documented night behaviors.

Pikas have been heard calling at night in previous field studies, implying nocturnal activity (Krear 1965, Smith 1974, Smith et al. 2016). Some Asian *Ochotona* species are known to be nocturnal (Kosaka et al. 1988, Sokolov et al. 2009), so it is not surprising that American pikas also would be active at night. Their relatively poor capacity for night vision, however, might compromise the benefits of nocturnal activity (Walls and Judd 1933). In the vicinity of the Bodie historic townsite, Smith (1974) reported nocturnal vocalizations that often exceeded the daytime rates, and at the same location, he observed night foraging and surface activity under a full moon. In their behavioral study at the south Mono Craters, Smith et al. (2016) reported surface activity and vocalizations at night during their periods of midsummer study (July 2014 and July 2015).

To our knowledge, only 3 studies have used trail cameras to survey behavior in pikas or to document diel activity. Massing (2012) used cameras to investigate nocturnal behavior at a low-elevation eastern Sierra Nevada talus for 2 weeks in October. Her cameras had variable success in capturing pika behavior, and they detected no evidence of nocturnal behavior. Hall and Calfoun (2019) documented nocturnal pika activity in the Rocky Mountains in Wyoming with camera traps. Camp et al. (2020) intensively studied diel behavior over the course of a summer (early June–early October 2017) by using field observations and trail cameras as well as by measuring talus temperatures at contrasting high-elevation (typical) and low-elevation (warm-margin, lava flow) pika locations in Idaho. They documented pika activity throughout 24-h periods, with suppressed midday activity and increased crepuscular behavior at the low-marginal site relative to the high-elevation site. Pikas at both sites were active and vocalized at night. Assessing diel behavior relative to talus temperatures, Camp et al. (2020) found strong correlation of temperature and pika activity at the low-elevation site: as surface temperature increased, surface activity decreased. The opposite was the case, however, at the high-elevation site, where surface temperature had no influence on activity. Smith (1974) reported similar patterns of diel activity between a pika population at the low-elevation, warm-marginal Bodie site compared with a high-elevation population in the Sierra Nevada. Elevated midday temperatures at these marginal sites led authors of both studies to conclude that pikas modified their behavior by retreating to cool talus matrices to avoid the hot surface (Smith 1974, Camp et al. 2020). Comparing these findings to the diel behavior of pikas and its relationship to temperature at our sites suggests that the sites where we assessed diel behavior and temperature might in fact not be marginal habitat for pikas. Since we had adequate numbers to assess only one of our extreme sites (WMM), this conclusion seems reasonable.

Additional Behaviors Documented by Cameras

Although many pika behaviors captured by our camera traps have been described previously, to our knowledge, published sequences of color photographs documenting these events have not been presented. Through photos in the manuscript figures and in the online image archive (see explanation on page 168), we hope to provide visual tools for education and further pika study. Our photos of other wildlife species visiting pika haypiles also document the capability of high-quality custom camera traps to enable accurate species identification (which allowed us to record the high diversity of species using talus environments and pika haypile positions) and to document interactions among individual pikas as well as between species. As in other studies (Smith et al. 2016), wounds and pelage markings allowed us to follow individuals among photographs without the need for tagging animals.

Descriptions of pika behaviors from field studies have been summarized in detail by Smith and Ivins (1983, 1984) and Smith and Weston (1990). Nonsocial behaviors we documented included cheek rubs, foraging, haying, locomotion, and surveillance. Previously described social behaviors that we documented included social tolerance (2 pikas sitting within 3 m of each other without an ensuing chase; Smith and Ivins 1984), vigilance, vocalization, and kleptoparasitism (McKechnie et al. 1994, Camp et al. 2020). Activities that generally occur beyond the haypile or outside the talus (chase, predator avoidance) obviously were not documented by our cameras. Several behaviors inferred from previous field observations or not previously described were directly captured by our camera traps. These behaviors included turnover of territory with disappearance of the adult resident and new occupation by a juvenile (Smith and Weston 1990, Smith 2001); winter behaviors, such as eating pieces of snow, licking icicles, winter night foraging, and resting on snow and ice; carrying sticks, dry pieces of wood, and caecotrophs; and eating fecal pellets.

Although we did not document direct predation events, we did photograph diverse predatory mammals hunting around the haypiles. In particular, we photographed weasels, skunks, ringtail, marten, and fox, as well as many species of Rodentia and Lagomorpha, on the haypiles and digging into them. Some of these species were obviously eating and removing vegetation in the photographs. To our knowledge, the only prior observation of haypile stealing by a sympatric species was an observation of a bushy-tailed woodrat taking vegetation from a haypile (Camp et al. 2020).

Conclusions

Our 5-year camera trap studies at 12 American pika sites demonstrated the effectiveness of custom camera traps in providing valuable information about pika site occupancy, animal behavior, and species diversity, while also rivaling or exceeding other methods. Our cameras photographed 4331 pika events, and documented not only field-observed behaviors that have been previously described, but also confirmed suspected or anecdotal observations and provided insights into new behaviors and novel interactions among animals. Importantly, camera traps documented active habitat occupancy by pikas (resident behavior) as well as transient use at sites we had previously evaluated as likely extirpated based on field surveys. These included sites at West Masonic Mountain in the northern Bodie Mountains and north Mono Craters. New behaviors documented in photos included a sequence showing turnover of a haypile from a mature resident pika to a juvenile; 2-pika kleptoparasitism where the resident appeared tolerant of the intruder; winter activity (during periods of snow cover) showing wintertime foraging, ice licking, and perching on rocks and snow at the haypile; and interactions with sympatric herbivores and predator species. Overall, 26 mammal species (including pika) and 10 bird species were documented by our camera traps, including 16 sympatric herbivores and 7 pika predators. Temperature surveys by mini-loggers at haypile sites and in talus matrices confirmed results of prior studies that indicate cool and stable temperatures of talus interiors, even on very hot summer days when external temperatures exceeded 35 °C. Considering that our sites were mostly warm, low-elevation pika habitats, such cool taluses likely provide important refuge from warming air temperatures. Although we documented pika activity at all hours of the day, including during crepuscular, midday, and nocturnal time periods, we found little evidence that pikas were more active during summer nights when preceding days were excessively warm. Pikas' capacity to be active throughout the day adds to their foraging success, as well as their resilience against predators, daily weather conditions and, likely, long-term climate change.

Documenting site occupancy and interactions with sympatric herbivores and predator species is important, especially for small mammal taxa such as pikas. In places where risks from climate change are a concern, camera traps provide valuable and relatively inexpensive simple approaches for wildlife studies, particularly for studies of small mammals that are vulnerable to changing climates.

SUPPLEMENTARY MATERIAL

Three online-only supplementary files accompany this article (https://scholarsarchive.byu.edu/wnan/vol81/iss2/1).

SUPPLEMENTARY MATERIAL 1. Species occurrence data by mountain range: Sierra Nevada, Bodie Mountains, and Mono Craters.

SUPPLEMENTARY MATERIAL 2. Summary of mean temperatures with standard deviations from dataloggers at pika sites where trail cameras were set.

SUPPLEMENTARY MATERIAL 3. Mono Basin mammal checklist; John Harris, Mills College, Oakland, CA; 20 July 2017.

ONLINE IMAGE ARCHIVE

A reference collection of 378 camera trap photographs of American pika behaviors and the sympatric species documented during the study, including comprehensive metadata, is available for free public use at the USDA Forest Service Research Data Archive, with the following citation:

HICKMAN, KENNETH T.; MILLAR, CONSTANCE I. 2020. Camera trap photographs from American pika haypiles in California. Forest Service Research Data Archive, Fort Collins, CO. https://doi.org/10.2737/RDS-2020-0039

ACKNOWLEDGMENTS

We thank Donald Grayson (University of Washington, Seattle), James Patton (University of California, Berkeley), Andrew Smith (Arizona State University), and Chris Wemmer (Smithsonian National Zoo) for sharing their expertise through many helpful discussions and for reviews of the draft manuscript (DG and AS). Reviews from Associate Editor Tim Karels and 2 anonymous reviewers improved the manuscript. We also thank Diane Delany and Bob Westfall (USFS–PSW) for help with graphics; Susan DesBaillets for field assistance; and Kipp E.B. Hickman and Kipp W. Hickman for cowriting the Exifgrabber software. The work was supported by operating funds from the USDA Forest Service to C.I. Millar.

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Received 9 July 2020
Revised 4 November 2020
Accepted 2 December 2020