

Geographic Variation in Vocalizations of American Pikas (*Ochotona princeps*) in
Southwestern Oregon and Northern California

by
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Abstract of Thesis

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The distribution of American pika (*Ochotona princeps*) populations in southwestern Oregon is poorly known and their range is highly fragmented. Isolated, small populations within this region are vulnerable to loss of genetic diversity and prone to extirpation. Vocalizations have been used to study connectedness among populations of pikas in other regions. Variation in calls may result from independent evolutionary or cultural histories and indicate the degree of isolation among populations. The purpose of this study was to determine if calls by individuals among different populations in the southern Cascades differ with respect to frequency and temporal features. Pika calls were recorded between May 2017 and April 2018 from six sites in the southern Cascades including Crater Lake National Park, Sky Lakes Wilderness, Mountain Lakes Wilderness, Cascade-Siskiyou National Monument (Vulture Rock and Surveyor Mountain), and Lava Beds National Monument. The populations at Vulture Rock and Sky Lakes Wilderness show significant difference in call features from those at Crater Lake. The differences in the calls of pikas from different sites in the southern Oregon Cascades suggest the populations are isolated and subject to further loss.

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Introduction

Dialect is defined as differences in vocalization between neighboring populations (Conner 1981 *vide* Nottebohm 1969). Geographic variation in calls includes differences in vocalization between populations distributed over long distances (Conner 1982) and has been studied in a variety of taxonomy groups including birds, anurans, cetaceans, primates, and rodents (Tyack 2008). One of the earliest studies of vocalization in small mammals involved pikas in the southern Rocky Mountains, where significant geographic variation was documented (Somers 1973). Studying vocalizations provides information about population isolation, evolution, behavioral diversity, and responses to habitat variation (Slobodchikoff and Coast 1980, Kroodsma et.al 1999, Pavlova et. al 2012, Keighley et al. 2017). Variation in vocalization may also be used to confirm subspecies or subpopulations (Hafner and Smith 2010, Pavlova et. al 2012). Human impacts such as habitat fragmentation, direct disturbance, introduced diseases, urbanization, chemical and noise pollution may influence animal acoustic behavior, including dialects, and potentially cause abnormal vocal responses (Laiolo 2010).

American pikas (*Ochotona princeps*), order Lagomorpha, are distributed throughout mountainous regions of Colorado, Oregon, Washington, Idaho, Montana, Wyoming, Nevada, California, New Mexico, and western Canada (Tolme 2005). Historically, *O. princeps* were divided into 36 subspecies, but recent molecular phylogenetic analysis indicates only five subspecies (Hafner and Smith 2010). The subspecies that is found in the Coast and Cascade Ranges is *Ochotona p. fenisex* (Hafner and Smith 2010).

Pikas are high-elevation animals, usually found above 3,000 m, but also occur at lower elevation at some locations in the southern region of their distribution, such as at Craters of the Moon National Monument and Preserve, Idaho, Lava Beds National Monument, California, and in the southern part of the Columbia River Gorge, Oregon (IUCN 2016). Recent discoveries of new populations in the northern Great Basin suggest

that pikas may be more common at low elevation in the region (Collins and Bauman 2012). They inhabit talus slopes (Luckman 2013) in alpine wilderness adjacent to meadows containing vegetations for foraging (Verts and Carraway 1998, Eder 2002). Talus slopes occur in weathering environment and are created by frost splitting in bedrock, subsequent ice melt, or degradation of alpine permafrost. Rock debris vary in size and shape, but mostly are angular (Luckman 2013). Occasionally, pikas inhabit man-made substrate such as mine tailings, roadcuts, and piles of scrap lumber (Smith 1974a,b, Manning and Hagar 2011, Waterhouse et al. 2017). At low elevation, pikas inhabit lava flows which provide climate refuges (Simpson 2009). Pikas do not make burrows but use spaces below boulders in the talus (Smith and Weston 1990). They locate their den and nest sites below rocks approximately 0.2 to 1 m in diameter (Smith and Weston 1990).

Smith (1974b) found that at high-altitude sites, pikas are active throughout the day, compared to at lower altitude sites, where they are more active in the morning and late afternoon. He also documented that pikas at lower elevation feed, call, and are more active throughout their territories at night, compared to those that inhabit high-altitude sites.

Pikas live in colonies, but they are nonsocial and territorial. A territory includes a single “hay pile” (Smith 1974a). Hay piles are accumulations of dried plant materials, gathered during summer for consumption during winter (Smith 1974a), that are stored under large boulders (Smith and Weston 1990). Pikas defend their territories by making distinct high-pitch calls, scent-marking, and aggressive chasing (Smith 1974a,b, Whitworth and Southwick 1984). Territory size varies from 410 m² to 790 m² and depends upon characteristics of the talus slope, distance from vegetation, and vegetation quality (Smith and Weston 1990).

American pikas are herbivores and they consume most plants available. However, they prefer plants with higher caloric, protein, lipid, and water content, such as green grasses (Poaceae family.), thistles (Asteraceae family), fireweed (*Chamaenerion spp.*), and sedges (*Carex spp.*) (Smith and Weston 1990). They collect forbs and tall grasses for haying while consuming short alpine grasses (Smith and Weston 1990). They have been

observed to collect plants with toxic concentrations in their hay piles and eat these plants after the decay of toxins (Wolf et al. 2007 *fide* Dearing 1997b). Like other Lagomorphs, pikas ingest their caecal pellets for extra nutrition either to directly consume or store them for later (Smith and Weston 1990).

Temperature is a significant factor that determines pika distribution (Verts and Carraway 1998). Pikas cannot tolerate heat due to their high metabolic rate, low thermal conductance, high resting body temperature, and low upper lethal body temperature (MacArthur and Wang 1974, Smith 1974*a*, Simpson 2009). Due to thermoregulation, pikas are usually restricted to boulder talus fields or lava flows that provide thermal refuge (Smith 1974*a,b*, Simpson 2009, Rodhouse et al. 2010). Low elevation populations are able to survive due to microclimates of complex lava flows and forb cover (Rodhouse et al. 2010). In the Columbia River Gorge, Oregon, pikas use unusual habitats such as dense, heavily shaded rainforest to remain active during the day (Beever et al. 2017).

The U.S. Fish and Wildlife Service was petitioned to list the American pika as threatened under the Endangered Species Act (Wolf et al 2007), although it is categorized as “Least Concern” by the International Union for Conservation Nature (IUCN 2016). However, climate change may have caused isolated pika populations in the Great Basin to become extinct (Beever et al. 2003), so their conservation status will likely change as climate change progresses. To find heat refuge, Pikas may be forced to move higher in elevation. With limited suitable habitat, increased competition, and discontinuous habitats, the risk of extinction will likely increase (Franken and Hik 2004, Tolmé 2005).

Pikas produce two different vocalizations, short calls and songs, and show geographic variation in them (Somers 1973, Conner 1982). The short call is a one-note or two-notes repeated call at intervals of 3 to 10 seconds (Somers 1973). They are the most common calls made while a pika sits on a boulder. Short calls have a variety of functions, such as alarm calls, territorial declaration calls, chase calls, and startle calls (Conner 1982 *fide* Krear 1965). Song is described by Somers (1973) as a series of 30-40 calls spaced closely in the beginning, and gradually lengthening the interval toward the end of the song.

The purpose of this study was to determine if calls by individuals among populations in southwestern Oregon and northern California differ with respect to structural features and frequency, to better understand connectedness of pika populations, and whether populations in the southern Cascades exhibit geographic variation. Variation in calls may result from independent evolutionary histories (Somer 1973) and indicate the degree of isolation among populations. Pika distribution is often limited by geographic barriers and temperature, (Conner 1982, Smith 1974*a*) which prevent the populations from interbreeding, increasing genetic loss, and risk of extinction (Smith 1974*a,b*, Smith 1987, Peacock and Smith 1997, Beever et al. 2003). This research is the first pika vocalizations study in the region. Two populations, Vulture Rock and Surveyor Mountain, were recently discovered, and are located in the Cascade-Siskiyou National Monument. Therefore, I hope this research will provide knowledge about the biogeography of isolated pika populations in the southern Cascades.

Methods

Study Sites

I attempted to collect data from six sites in southern Cascades region; 5 in Oregon, and 1 in California. I chose the farthest north and the farthest south pika habitats that I could access. The additional sites between the north and the south sites were selected based on data from biologists who had information of pika populations in the Cascades region. The sites in Oregon were rockfall talus and the California site was a lava flow (Fig. 1).

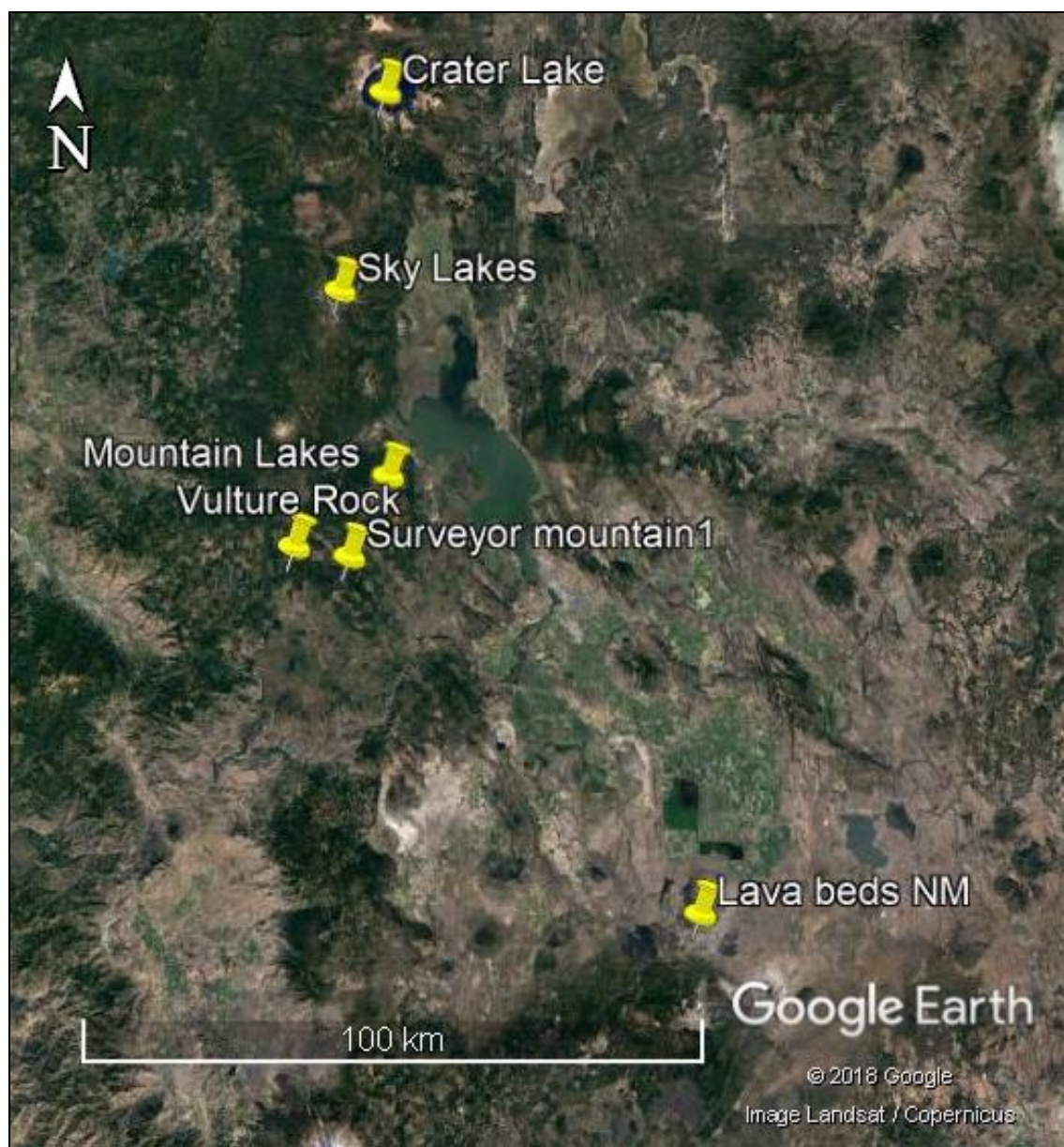


Fig. 1. Map of pika vocalizations study sites in the southern Cascades region, 2017. Crater Lake (CL), Sky Lakes (SL), Mountain Lakes (ML), Vulture Rock (VR), and Surveyor Mountain (SM) were in the state of Oregon, and Lava Beds (LB) was in the state of California. Map data: Google Earth.

Crater Lake (CL)

The Crater Lake site (Fig. 2) was located in the Crater Lake National Park on East Rim Drive, across the road from the Park Headquarters parking lot (42.897°N, 122.131°W). The site could be accessed from the Castle Crest Wildflower Garden Trail. The elevation at the site ranged from 1,981 – 2,134 m. Average daily high temperature in August is 21°C. Dominant trees surrounding the site were red fir (*Abies magnifica*) and mountain hemlock (*Tsuga mertensiana*). The dominant plants found at the open area where the edge of the forest met the slope were scarlet gilia (*Ipomopsis aggregata*), goldenweed (*Pyrrocoma spp.*), and sulphur buckwheat (*Eriogonum umbellatum*).

Pikas inhabited the entire west-facing mountain slope, and I recorded as many individuals as I could from every direction and elevation of the mountain face, approximately 14 ha.



Fig. 2. Photograph of the CL study site, August 2017, Crater Lake National Park, Oregon. The open area at the edge of the forest was covered with boulders, grasses, and ground-cover plants.

Sky Lakes (SL)

The Sky Lakes site was located in the Sky Lakes Wilderness in the Fremont-Winema National Forest near Crater Lake National Park, Oregon. The wilderness area is 45,968 ha and ranges from the Crater Lake National Park south to Highway 140. To increase sample size, I recorded the vocalizations from two locations within the study area. The first location was near Margurette Lake (42.602° N, 122.202° W) on the east side of the wilderness. The second unit was by Snow Lake and Luther Mountain (42.612° N, 112.207W), 1.3 km north from Margurette Lake. The elevations are 1,839 m and 2,146 m at Margurette Lake and Snow Lake, respectively (Fig. 3). Edges of the talus slopes at both sample units were adjacent to a body of water (Margurette Lake and Snow Lakes) with a high percentage of canopy cover (Fig. 4). The dominant trees found on the talus edges were red fir, mountain hemlock, and subalpine fir (*A. lasiocarpa*). Quaking aspen (*Populus tremuloides*) occurred around the lakes.

Sampling locations covered approximately 9 ha at Margurette Lake and 5 ha at Snow Lake. The Snow Lake slope was inaccessible due to high water level and downed logs. I recorded the vocalizations from across the lake. The slope at Margurette Lake faces southeast, while the site at Snow Lake faces northeast.



Fig. 3. Map of sampling units in SL indicated by the red circles. The yellow pins indicate important landmarks in the map, Sky Lakes Wilderness, Klamath Falls, Oregon. Map data: Google Earth.



Fig. 4. Photograph of the talus slope by Margurette Lake at the SL site, August 2017, Sky Lakes Wilderness, Klamath Falls, Oregon.

Mountain Lakes (ML)

This site was located in the Mountain Lakes Wilderness, in the Fremont Winema National Forest near Klamath Falls, Oregon (Fig 5). The wilderness includes a total of 9,337 ha and is located in the southern portion of Sky Lakes Wilderness. My sample site was located on the west side of Lake Harriette (42.338° N, 122.102° W) at an elevation of 2,103 m. The talus slope covers approximately 4.5 ha and faces northeast. The dominant trees found on the site were red fir, mountain hemlock. Whitebark pine (*Pinus albicaulis*) were also found at the site.



Fig. 5. Photograph of talus slope at the ML site, July 2017, Mountain Lakes Wilderness, Klamath Falls, Oregon.

Vulture Rock (VR)

This site was on the west side of Vulture Rock (Fig. 6) located in the Cascade-Siskiyou National Monument (CSNM) (42.239°N, 122.300°W). Vulture Rock is largely a talus outcrop at an elevation range of 1,800 – 1,830 m. The edge of the slope was dominated by shrub-form golden chinkapin (*Chyrsolepsis chrysophylla*), and the dominant trees in the surrounding area were red fir, Douglas-fir (*Pseudotsuga manziesii*), and white fir (*Abies concolor*). VR was the smallest site of the six study sites. I recorded calls from west and southwest sides of the rock due to inaccessibility of the other sides.



Fig. 6. Photograph of the VR site on the west slope, April 2018.

Surveyor Mountain (SM)

The Surveyor Mountain site included a series of outcrop rocks oriented roughly from north to south, in the CSNM and had two study units which were the two biggest outcrops. The first unit was at the second outcrop from the north of the Surveyor Mountain (42.225°N , 122.191°W), and the second unit was 1.56 km south of the first unit. (42.213°N , 122.181°W). The elevation and area at the first and second units were 1,945 m and 0.82 ha, and 1,987 m and 1.0 ha, respectively. The dominant trees included Douglas-fir, red fir, and white fir.

Lava Beds (LB)

This site was located in the Lava Beds National Monument (LBE), California (41.714°N, 121.510°W) and was the southernmost site and was markedly different from other sites in terms of elevation, substrate, and temperature. LB had the lowest elevation of all the sites (approximately 1,524 m) and had diverse landscapes including lava flows, caves, and talus slopes (buttes). The pika population at LB inhabited unique habitats within the lava flows (Fig. 7). The climate at the site is much hotter and drier than most sites occupied by pikas, with average summer high temperatures between 24 – 26°C (Rodhouse, 2017).

I visited all potential habitat in LBE; lava flows (Devil's Homestead, and Schonchin Flow), caves (Cave loop), and talus slopes (Schonchin Butte) (Fig. 8). I selected habitats based on the "Pikas in Peril" research (Rodhouse 2017). I visited the site eight times from May 2017 through April 2018 and conducted field surveys lasting from 1 to 5 hours, in at least two different habitats. At lava flows and cave habitats, I walked across the landscapes for approximately 45 minutes to prompt the pikas to call. Then, I remained at one spot for 30 minutes – 2 hours and waited for the pikas to call. At the talus slopes, I applied a method "sit and wait" for 1-3 hours. The total area visited was approximately 122 ha. The main vegetation found at all habitats was grasses, western juniper (*Juniperus occidentalis*), big sagebrush (*Artemisia tridentata*), and gray rabbitbrush (*Ericameria nauseosa*).



Fig. 7. Photograph of lava flow at the Devil's Homestead, November 2017, Lava Beds National Monument, California. Devil's Homestead was one of the study units at the LB site.

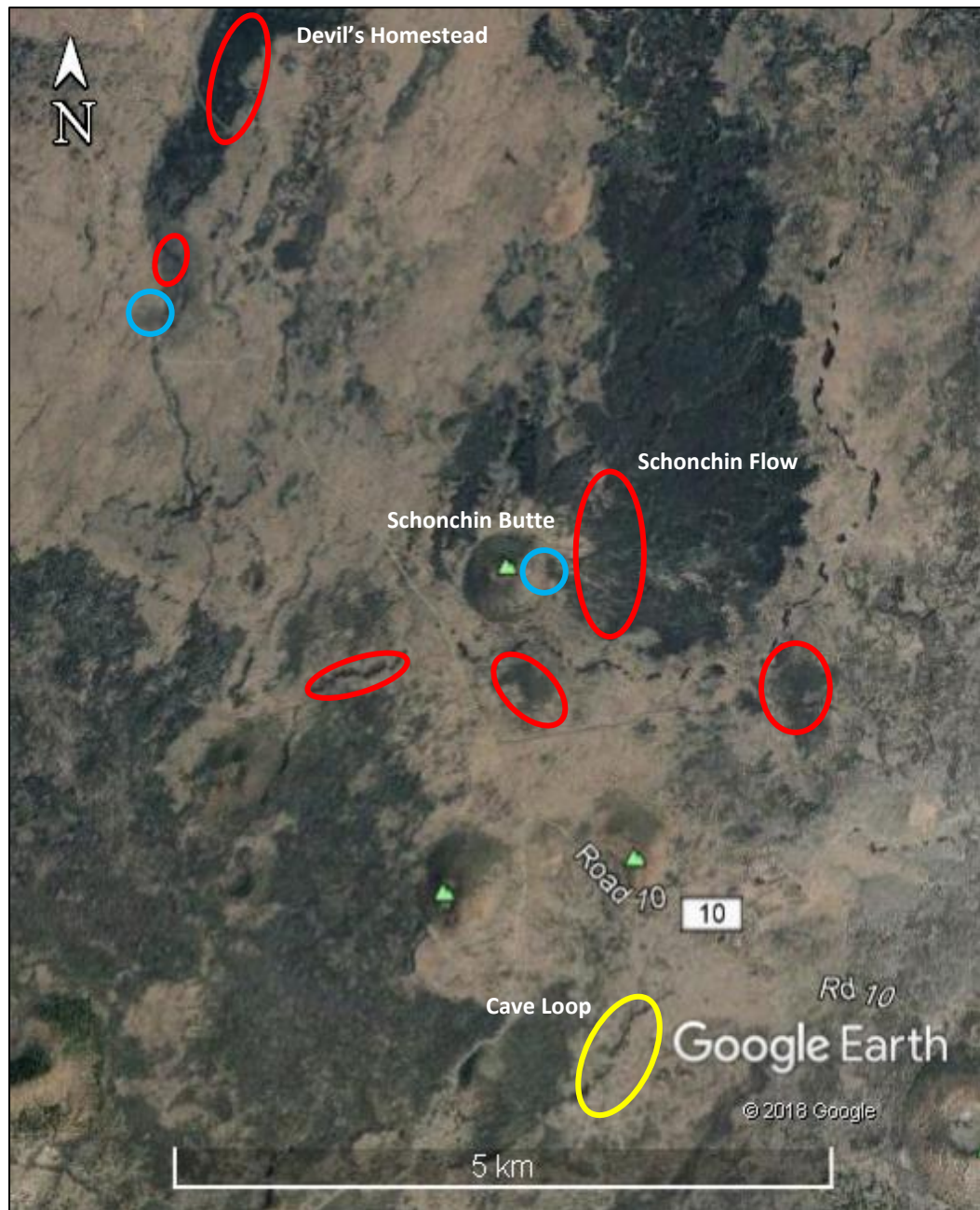


Fig. 8. Aerial image of the LB site. Colored circles indicate locations I visited to record pika vocalizations from May 2017 – April 2018. Red circles indicate lava flows, blue circles indicate talus slopes, and the yellow circle indicates lava caves area. Map data: Google Earth.

Field Methods

I recorded pika vocalizations from May 2017 through April 2018. I conducted the surveys mostly in the morning between 7:00-11:00 (Pacific Standard Time) when the pikas were most active (Somers 1973, Conner 1982). When the recordings during the morning surveys did not provide sufficient data, I conducted the surveys again between 14:00 – 18:00 when the pikas were most active in the afternoon.

I used a Marantz PMD660 digital recorder coupled with a Sennheiser ME-62 microphone in a 61 cm parabolic reflector to record short calls when pikas defended their territories or when they felt threatened. American pikas produce short calls for territorial defense calls and alarm calls (Somers 1973 *vide* Krear 1965). I also recorded songs, but did not analyze them. The song is a series of 30-40 calls spaced closely in the beginning, and gradually lengthening the interval toward the end of the song (Somers 1973). Pikas usually shifted from a song to short calls. The short calls that were generated after the songs were also analyzed.

When I approached a talus slope, I selected an open, clear spot where I could turn 180 degrees and get clear recordings without obstacles. I remained for 30 mins – 3 hours at each spot, depending on how active the pikas were. If they were active, I would move to adjacent locations after about 30 minutes to record as many individuals as possible. I only recorded calls from unseen individuals when I was confident that the calls were from different individuals based on distance and territories (Keighley et al. 2017). Also, I had a research volunteer keeping track of other calls' distances and directions while I recorded a call. If the pikas were not active, I would approach the slopes to provoke the pikas. I recorded times and directions of the calls in a field note along with track numbers as references for sound analysis processes.

I installed a Reconyx HC600 Hyperfire Covert trail camera and a Roland R-05 MP3 recorder equipped with an Olympus ME51S microphone, 2 Urbanti 100mm funnels, a 40Ah 3.2V LiFePO4 battery, and a modified Pelican case at VR site from 28 June – 7 July 2017 to attempt to determine when the pikas were most active during the day.

Call Features and Classification

I used Raven Pro: Interactive Sound Analysis Software version 1.5 (Raven Pro 1.5, Bioacoustics Research Program, The Cornell Lab of Ornithology, Ithaca, NY) to convert sound files (wave) into spectrograms. I used Hann window, DFT = 512 samples with 50% frame overlap. I measured fundamental frequencies, the lowest frequency in sound, and dominant frequencies, a frequency with the highest amplitude in a sound, of a call (Hopp et al. 1998) (Fig. 9). I selected ten variables composed of time and frequency features to evaluate the difference between the calls (Table 1 and Fig. 10). To reduce bias and errors, I was the only one analyzing the data.

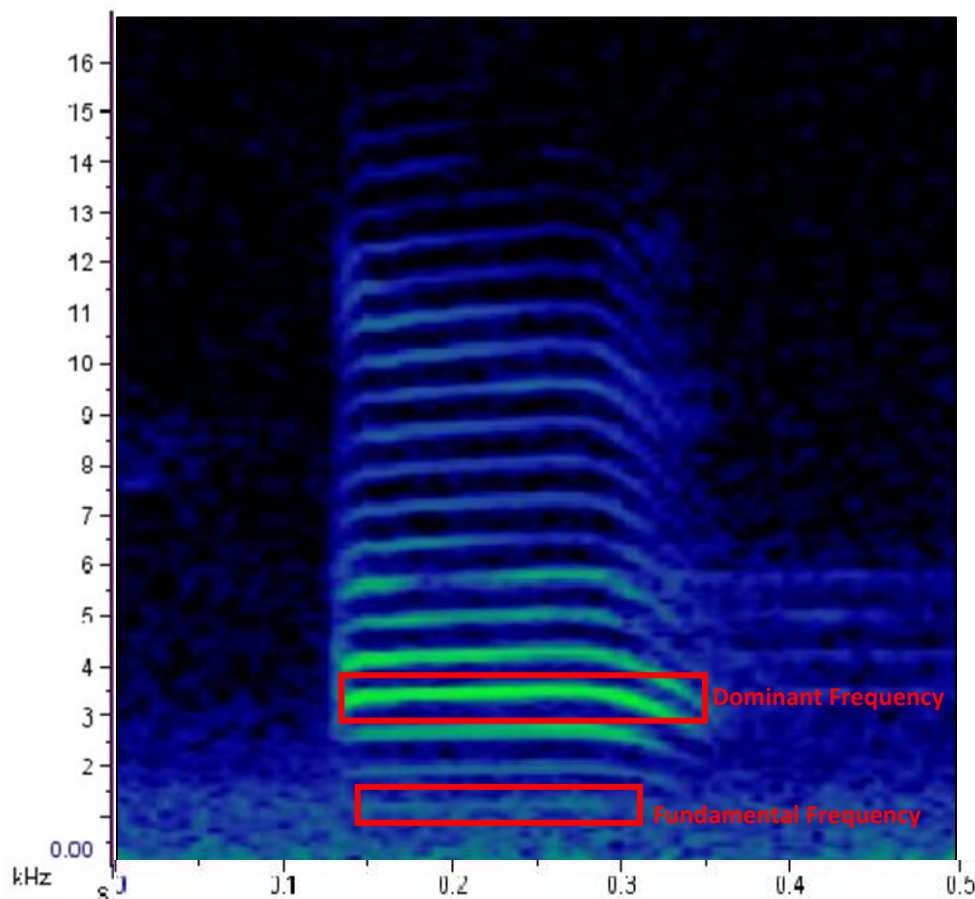


Fig. 9. A spectrogram of a pika short call. The figure shows a fundamental frequency and a dominant frequency. The units are kHz (Kilo Hertz) for frequency and S (Second) for time.

Table 1. The variables used to analyze the differences in pika vocalizations with their descriptions. See Appendix.

Variables	Description
$\Delta\text{funfreq}$	A difference between minimum and maximum frequency (Hz) of a fundamental frequency
$M\text{funfreq}$	A mean frequency (Hz) of a fundamental frequency
$\Delta\text{domfreq}$	A difference between minimum and maximum frequency (Hz) of a dominant frequency
$M\text{domfreq}$	A mean frequency (Hz) of a dominant frequency
$T\text{domfreq}$	A time duration (s) of a dominant frequency
$\Delta\text{inimaxdomfreq}$	A difference between initial and maximum frequency (Hz) of a dominant frequency
$\Delta\text{maxfindomfreq}$	A difference between maximum and final frequency (Hz) of a dominant frequency
$T\text{maxfindomfreq}$	A duration in time from maximum frequency to final frequency (s) of a dominant frequency
$T\text{iniflucdomfreq}$	A duration in time from initial frequency to the first fluctuation point (s) of a dominant frequency
$T\text{inimaxdomfreq}$	A duration in time from initial frequency to maximum frequency (s) of a dominant frequency

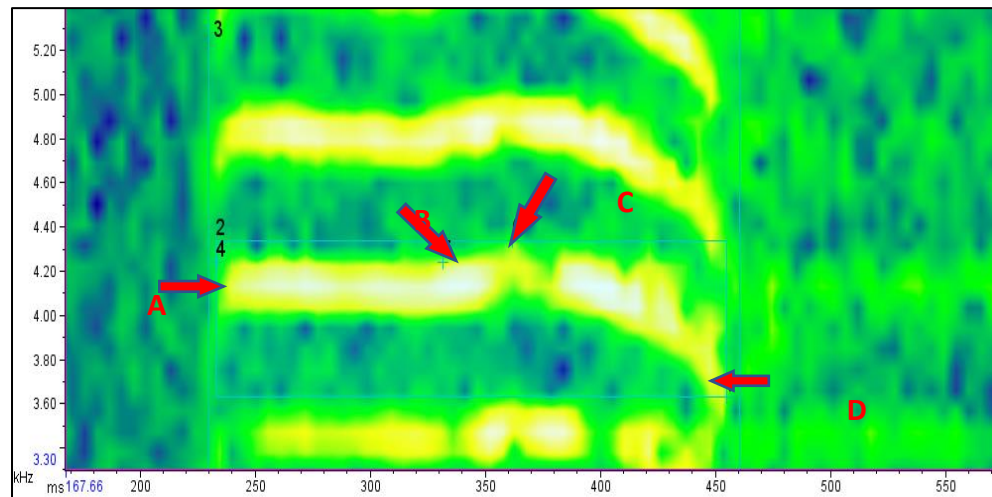


Fig. 10. The dominant frequency of a short call. Letters A, B, C, and D identify initial frequency, fluctuation point, maximum frequency, and final/minimum frequency, respectively. Note that the minimum and final frequencies are not always the same.

Data Analysis

I measured 120 of 138 spectrograms. The exceptions were the spectrograms that had low power, showed incomplete characteristics, or overlapped with background noises. I created a data sheet to compile spectrogram data from every site. The data were categorized by individual pikas. After I measured the spectrogram, I selected a representative call from each individual to analyze. A representative call of a pika was the call that showcased the primary characteristics of the individual's calls with the clearest spectrogram. Also, I excluded from statistical analysis the data from sites with a sample size less than three.

Prior to inclusion into the Principal Component Analysis (PCA), I tested the normality of each variable. It was necessary to log-transform three variables (*Δ*funfreq, *T*domfreq, and *M*funfreq) to meet the assumptions of the PCA. I used PCA to analyze the variables extracted from the calls to reveal patterns suitable for further analysis. I then analyzed the PCA score using an analysis of variance (ANOVA) to evaluate differences in calls among populations using the 95% confidential interval as the level of significance for all tests. I used a Tukey post hoc test to determine significant differences between sites. The descriptive statistics were also performed on ten variables in order to explain the characteristics of the vocalization from each site. All the statistical analysis performances were using Statistica 7.1 (StatSoft, Inc., Tulsa, OK).

Results

I recorded thirty-nine individual pikas from the six sites (Table 2). Data from ML, SM, and LB were excluded from further analysis due to small sample sizes. I found old pika scat at the SM site, but there was no evidence to support the existence of a current pika population at any of nine outcrops on Surveyor Mountain (Brown 2017). At LB, where the site was vast and composed of many habitats, the pika activity was very low and no vocalizations were heard or recorded. Pika activities at ML were also low. I was able to record only four vocalizations from two individual pikas from the ML site.

PCA results from CR, SL, and VR populations identified four Principal Component Factors that best explained the variations in call structure and frequency. The four factors with eigenvalues >1 were considered for further analysis. The cumulative percentages of variance of the first four factors were 76.5% (Table 3).

The first four factors were individually tested with ANOVA to evaluate the difference in variance in calls among populations. The calls among three populations differed along the first factor component (PC1), but there was no difference in vocalizations among populations along PC2, PC3, and PC4 (Table 4).

I completed a Tukey test to understand which populations differed from the others. The Tukey test showed that vocalization of the pika populations at VR and SL differed from those at CL ($p = 0.006$ and $p = 0.03$, respectively). The vocalizations from populations at VR and SL were not significantly different. Factor scores from PC1 suggested that the variables that had strongest correlations with the factor were $\Delta\text{domfreq}$, $\Delta\text{inimaxdomfreq}$, $\Delta\text{maxfindomfreq}$, $T\text{iniflucdomfreq}$, and $T\text{inimaxdomfreq}$ as indicated by the magnitude of the correlations of these variables with PC1 (Table 3). These variables described the magnitude with the frequency changes, and the length of a dominant frequency within the call. Means of the five variables on the PC1 axis were higher at the CL site than the others, and the VR site had the lowest mean values (Table

5). The results suggested that the calls from the CL population provided broader and longer parabolic shape dominant frequency bands (Fig. 11).

The trail camera installed at the VR site captured photos of a pika on the southwest side of the rock. It was the first photograph of the pika population in the CSNM. I acquired 215 hours of sound records from the Roland digital recorder. Unfortunately, I was unable to process them due to technical problems. The photographs from the trail camera suggested that the active times of the pika were 7:00 – 11:00 and 14:30 – 16:00. However, this only applied to one pika on the southwest side of Vulture Rock.

Table 2. Number of individual pikas recorded, average temperature during data collection, slope aspects, and elevation at each site from June – Nov 2017.

Site	Number of individuals recorded	Average Temperature (°C)	Slope aspect	Elevation (m.)
Crater Lake (CL)	17	23	Western	1,981 – 2,134
Sky Lakes (SL)	15	22	Southeastern, northeastern*	1,839; 2,146*
Mountain Lakes (ML)	2	18	Northeastern	2,103
Vulture Rock (VR)	5	15	Southwestern	1,800
Surveyor Mountain (SM)	0	16	Eastern on both units	1,945; 1,987**
Lava Beds (LB)	0	24 – 26***	-	1,524
Total	39			

* Margurette Lake and Snow Lake, respectively

**First unit and second unit, respectively

*** Average temperature in summer

- Data not available

Table 3. Factor score coefficients, based on correlations of variables with each factor, and eigenvalues of the first four factor components (PC) from PCA analysis that best explain the variables of call structures and frequencies of the pika populations at CR, SL, and VR. Bold face numbers represent variables with the strongest correlation with each PC.

Variables	PC1	PC2	PC3	PC4
Δ domfreq	0.275	0.242	-0.020	-0.165
Mdomfreq	-0.053	-0.059	0.503	-0.320
Δ inimaxdomfreq	0.208	-0.234	0.036	-0.062
Δ maxfindomfreq	0.254	0.288	-0.027	-0.153
Tmaxfindomfreq	0.086	0.205	0.495	0.010
Tiniflucdomfreq	0.253	-0.186	0.109	0.282
Tinimaxdomfreq	0.234	-0.267	-0.006	0.324
Mfunfreq	-0.074	-0.314	0.093	-0.408
Tdomfreq	-0.055	-0.027	0.393	0.349
Δ funfreq	0.176	-0.153	-0.050	-0.449
Eigenvalue	2.84	2.13	1.47	1.20
Percentage of Variance Explained	28.4%	21.3%	14.7%	12.0%
Cumulative Percentage of Variance	28.4%	49.7%	64.5%	76.5%

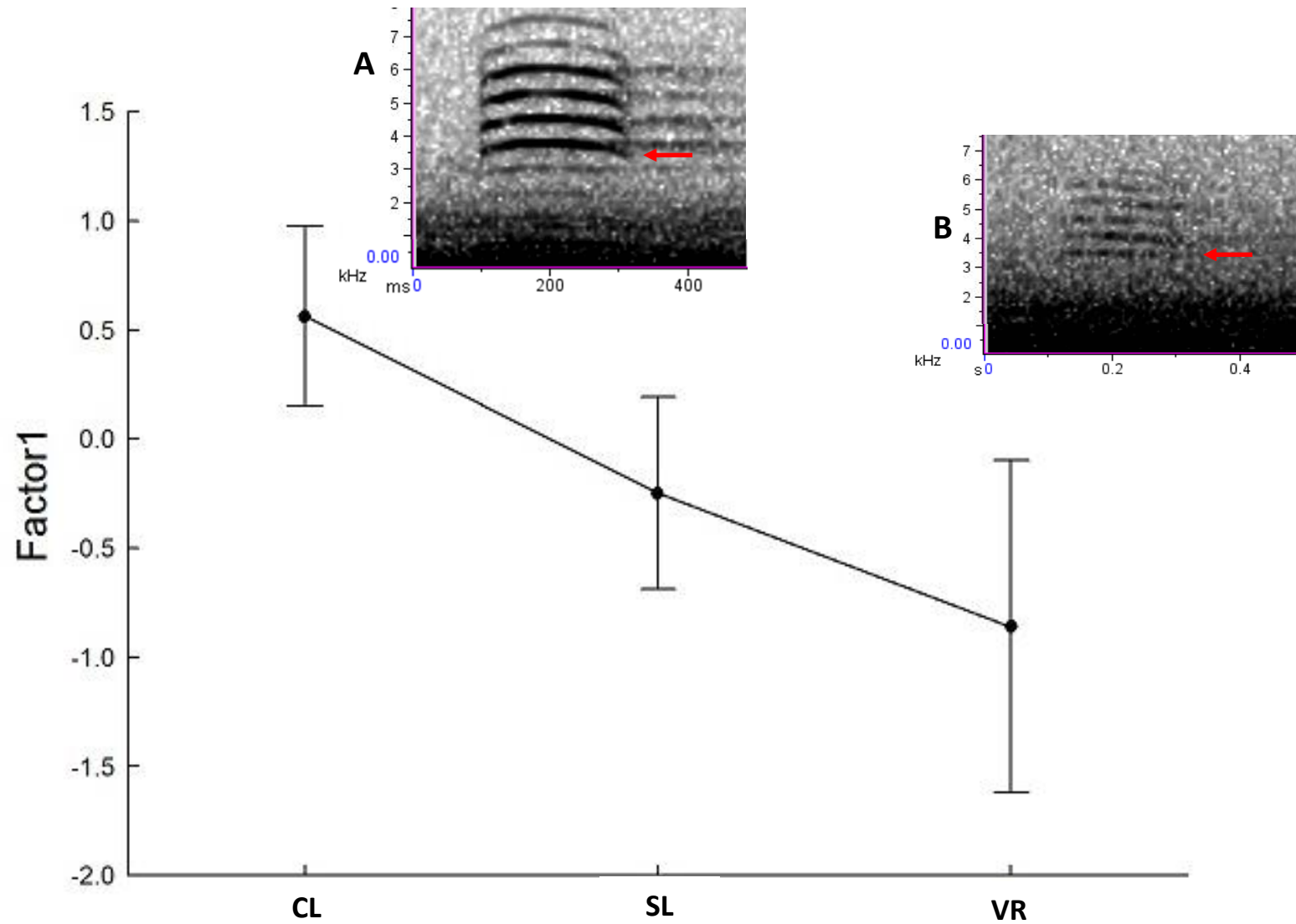


Fig. 11. Mean factor score values along PC1 ($\pm$ SE) among three sites. Figure A and B are representative pika calls from CR and VR populations, respectively. The red arrows identify dominant frequencies of the calls. The calls from VR and SL showed significant different mean value from those at CL.

Table 4. One-way ANOVA of call structures and frequencies along each factor.

Factor Component	df	SS	MS	<i>F</i>	<i>p</i>
PC1	2, 34	9.93	4.97	7.06	0.003*
PC2	2, 34	3.59	1.80	1.89	0.167
PC3	2, 34	1.15	0.76	0.73	0.491
PC4	2, 34	3.86	1.93	1.96	0.156

Table 5. Means ($\pm$ SE) of variables of the pika calls among three sites. Bold face variables represent variables with the strongest correlation on PC1's factor score.

Variables	Mean ($\pm$ SE)		
	CR (N=17)	SL (N=15)	VR (N=5)
Δdomfreq (Hz)	691.28 ($\pm$ 42.93)	602.62 ($\pm$ 59.65)	455.70 ($\pm$ 61.21)
Mdomfreq (Hz)	3,664.97 ($\pm$ 126.46)	3,673.13 ($\pm$ 77.35)	4,098.06 ($\pm$ 121.36)
Δinimaxdomfreq (Hz)	421.10 ($\pm$ 51.39)	248.86 ($\pm$ 54.68)	351.22 ($\pm$ 96.16)
Δmaxfindomfreq (Hz)	630.19 ($\pm$ 61.16)	487.69 ($\pm$ 87.49)	246.12 ($\pm$ 110.83)
Tmaxfindomfreq (sec)	0.105 ($\pm$ 0.01)	0.112 ($\pm$ 0.02)	0.115 ($\pm$ 0.04)
Tiniflucdomfreq (sec)	0.074 ($\pm$ 0.01)	0.048 ($\pm$ 0.01)	0.030 ($\pm$ 0.01)
Tinimaxdomfreq (sec)	0.074 ($\pm$ 0.01)	0.045 ($\pm$ 0.02)	0.030 ($\pm$ 0.01)
Mfunfreq (Hz)	2,238.08 ($\pm$ 208.00)	1,679.64 ($\pm$ 302.00)	3,010.96 ($\pm$ 447.46)
Tdomfreq (sec)	0.179 ($\pm$ 0.01)	0.201 ($\pm$ 0.03)	0.186 ($\pm$ 0.02)
Δ funfreq (Hz)	384.15 ($\pm$ 41.70)	284.83 ($\pm$ 12.47)	293.14 ($\pm$ 33.10)

Discussion

Vocalizations of American Pikas differed among three populations in the southern Cascades. The post-hoc analysis showed that the vocalizations of the Sky Lakes and Vulture Rock populations differed from those at Crater Lake. The results suggested that the pika population at Crater Lake generated more complicated calls, showing more arc, more fluctuation points within a dominant frequency band, and more harmonics compared to those at Sky Lakes and Vulture Rock, which showed less arc or straight line, few changes within a dominant frequency band, and few harmonics (Fig. 11). Differences in call structures and frequencies indicated that pikas in the southern Cascades region display geographic variation in vocalizations between populations. The results suggested the populations have become isolated. Geographic variation in vocalizations of the species also occurred in Rocky Mountain and Great Basin populations (Somes 1973, Conner 1982).

Pikas are poor dispersers (Smith 1974*a,b*). At low-elevation sites, juveniles are not likely to disperse more than 300 m (Smith 1974*a*). Dispersal success is mainly influenced by temperature and availability of continuous habitats (talus patches). Low dispersal success can influence isolation of the populations. This limitation may cause inbreeding and low levels of genetic variation, which may lead to local extirpation (Smith 1974*a,b*, Smith 1987, Peacock and Smith 1997, Beever et al. 2003).

Temperature, especially during summer, was one of the main factors influencing the success of juvenile dispersal (Smith 1974*b*, Beever 2010, Calkins et al. 2012). Henry et al. (2012) found a relationship between patterns of genetic variation and climatic factors which indicated that climate change may reduce dispersal success. Historical evidence also shows that pika distribution and genetic diversification were influenced by glaciation and interglacial periods (Grayson 2005, Galbreath et al. 2009). The results of climatic effect on population decline in southern populations (Sierra Nevada, Central

Utah, and Southern Rocky Mountains) can already be detected at the genetic level (Galbreath et al. 2009). A result from a study by Galbreath et al. (2009) using Bayesian skyline plots for all American pika lineages showed a negative trend in median effective population size since the Large Glacial Maximum, approximately 20,000 years ago. Additionally, the dispersal successes of pikas may be limited by landscape heterogeneity and aggressive behavioral by resident adults toward juveniles (Robson et al. 2015).

Climate change may affect pika distribution. The most dramatic change predicted by the species-distribution model developed by Calkins et al. (2012) is that when global temperature increases 7°C, more than half of the pika subspecies are predicted to lose >98% of their habitats (Calkins et al. 2012). Also, increasing temperature and the rate of increase may result in faster population loss than that represented by the historical records (Beever et al. 2003). Pikas response to climate change is difficult to generalize and will likely differ among locations (Schwalm et al. 2016).

Habitat idiosyncrasies, such as microclimate refuges provided by the physical features of the habitat, vegetation, and habitat connectivity, are the main factors that will determine the extent of climate impacts on pika populations (Simpson 2009, Millar and Westfall 2010, Jeffress et al. 2013, Hall et al. 2016, and Schwalm et al. 2016). Because pika populations in the southern Cascades are isolated, they are likely to be at risk of extirpation due to climate change. Climate warming may decrease connectivity among populations (Castillo et al. 2014) and shift relative abundances of food plants (Beever et al. 2003). The severity of these impacts will be site-specific and strongly dependent on habitat-mediated microclimates (Millar and Westfall 2010), and forage availability (Jeffress et al. 2013). Therefore, in order to understand the impacts of climate change on the populations, more data and an accurate model is needed to predict microclimate and other site-specific variables, rather than using a large-scale model (Schwalm et al. 2016).

Pika populations in the southern Cascades show different levels of complexity in calls. Among birds, complex songs are more effective in territorial defense (Rogers and Kaplan 2000). At Crater Lake, the pikas may produce more complex calls than the other sites due to high population density; they need to defend their territories from many neighbors. Alarm call complexity also plays a role in individual recognition (Rogers and

Kaplan 2000). Group members may refuse to respond to an unreliable caller who often makes false calls. In contrast, group members may respond faster to a reliable signaler (Rogers and Kaplan 2000 *fide* Hare 1998). The relationship between group size and vocal complexity is also found in rodent species (Blumstein and Armitage 1997, Lima et al. 2018). Animals with complex social systems usually have more complex communication systems, compared to those with simple or no social systems (Freeberg et al. 2012). Although pikas don't have complex social systems, they live in colonies in insular habitats. The pikas at CL interact with other individuals more than the pikas at the other sites and this may cause them to develop more complex calls.

Relationships between habitat characteristics and call complexity have been studied in many species including primates, birds, and rodents (Slobodchikoff and Coast 1980, Slabbekoorn and Smith 2002, Tyack 2008). Animals select specific vocalizations to send signals (i.e. territorial defense, warning, attracting mates) to a receiver through various habitat types, consisting of different ambient noise and sound transmission characteristics (Morton 1975, Slabbekoorn and Smith 2002). As a result, different environments lead to signals with different characteristics within same species that live in different habitats (Freeberg et al. 2012 *fide* Endler 1992). A study of Gunnison's prairie dogs (*Cynomys gunnisoni*) shows that more complex calls, represented by more syllables per call and longer call length, are given where shrubs, rocks, and tree stumps were present. Less complex calls are given by prairie dogs living in an open grassland (Slobodchikoff and Coast 1980). Birds living in dense forest produce songs with a lower average frequency than those that live in open habitats (Morton 1975, Slabbekoorn and Smith 2002). Although habitat characteristics of three of my study sites appear to be similar, microhabitat characteristics and abiotic factors such as wind direction, adjacent terrain, surrounding trees, and shrubs may influence the difference in vocalizations at each site.

Slabbekoorn and Peet (2003) reported that great-tits (*Parus major*) in noisy urban areas sang at higher frequency than those in quiet neighborhoods. This may explain the wider range of dominant frequencies in pika calls at the Crater Lake, where the background noise was significantly higher than at the other sites. The Crater Lake site

was near the East Rim Drive, and traffic noises were heard during the period of observation. However, differences in vocalization structures are not always determined by different habitat characteristics (Slabbekoorn and Smith 2002). Moreover, biological factors such as body size, sex, and age could also lead to differences in vocalization (Tyack 2008 *fide* Mitani et al. 1999). For example, if age ratio differed among populations, it might lead to the differences in mean call frequencies among sites and generate misinterpretation of the observed geographic variation.

Many studies have explored the genetic basis of vocalization in birds (Catchpole and Slater 1995, Wright and Wilkinson 2001, Soha et al. 2004, Ribot et al. 2012) but there have been few studies in mammals. Early studies provided ambiguous and vague results of a relationship between gene flow and variation in vocalizations (Catchpole and Slater 1995). One difficulty is separating genetic from a cultural influences, and recent studies have produced mixed results - either there are positive relationships between restricted gene flow and vocal variations (MacDougall-Shackleton and MacDougall-Shackleton 2001, Ribot et al 2012) or gene flow and dialects are not correlated (Wright and Wilkinson 2001, Soha et al 2004). In sperm whales (*Physeter microcephalus*), there is a positive correlation between vocalization and mitochondrial haplotype without influence from geographic variation (Whitehead et al. 1998, Rendell et al. 2012).

Pika extinction has been predicted as the global temperature continue to rise (Beever et al. 2003). I found no evidence of a current population at Surveyor Mountain, Cascade-Siskiyou National Monument. Degraded feces were located indicating relatively recent occupation, likely within the last decade (Brown 2017). Habitat turnover (Extirpation and recolonization) occurs in pika populations (Smith 1980, Smith and Nagy 2015), but recolonization success rates are negatively related with distance between habitats (Smith 1974a, 1980). The relative isolation of the site will make recolonization unlikely. The distance from Vulture Rock to Surveyor Mountain is 8,780 m, while juvenile pikas are not likely to disperse greater than 300m (Smith 1974a). Also, anthropogenic barriers such as Keno Access Road combine with lack of habitat connectivity to prevent pikas from dispersing (Beever et al. 2003, Waterhouse et al.

2017). However, more intensive study of Surveyor Mountain is needed before concluding the population no longer exists and the causes of its loss.

The pikas at Vulture Rock are unique, with a small population size. I recorded five individual pikas at the site. It's common that most pika habitats contain fewer individuals than the carrying capacity of the site (Smith 1974a, 1980) and it is possible that there are more pikas at Vulture Rock than I recorded. However, with a small number of individuals, and isolation, combined with rising temperature limiting emigration and immigration, the Vulture Rock pikas and the populations of southern Cascades are vulnerable to loss of genetic diversity. Further extirpation and more isolation among populations can be expected. Conservation and habitat management should focus on maintaining habitat connectivity to reduce the risk of extirpation of small isolated populations.

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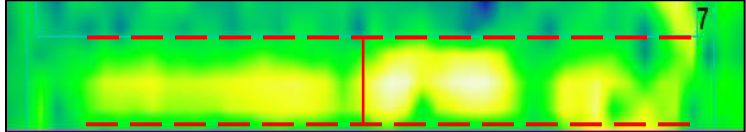
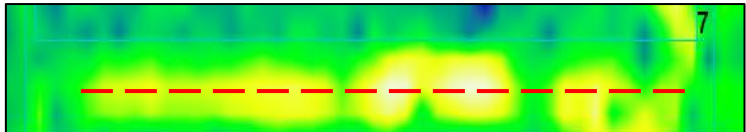
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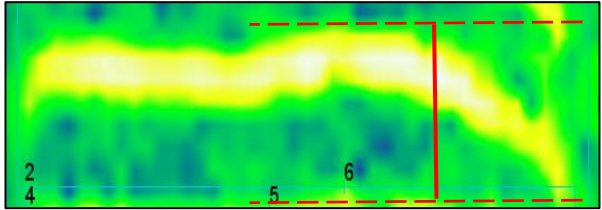
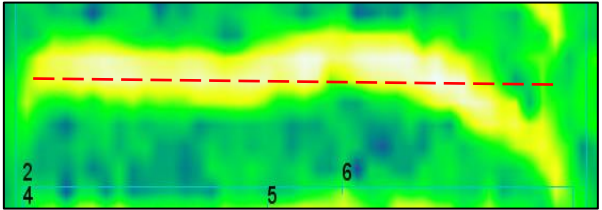
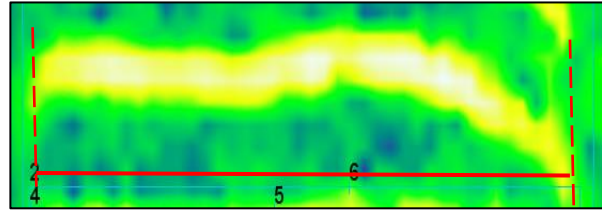
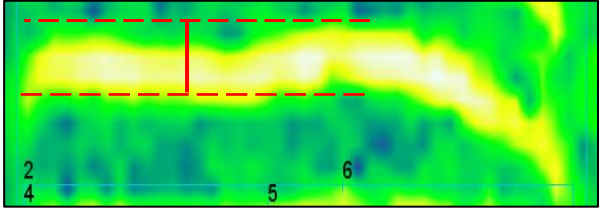
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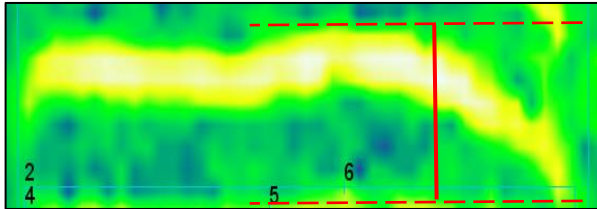
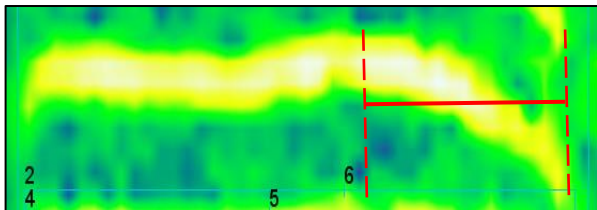
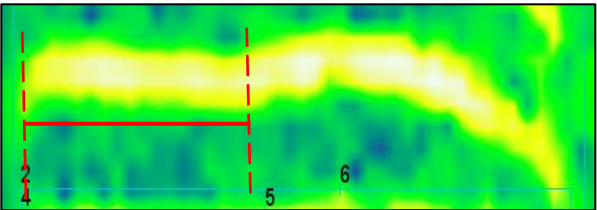
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Appendix: Examples of variables' measurement

Table 6. Example figures of each variable's measurement. Dash lines show directions of the measurements. Solid lines show distance of the measurements.

Variables	Description	Figures
$\Delta\text{funfreq}$	A difference between minimum and maximum frequency (Hz) of a fundamental frequency	 A spectrogram showing frequency content over time. Two horizontal dashed red lines are drawn across the plot, one above the other, indicating the minimum and maximum frequency of a fundamental frequency. A vertical solid red line segment connects these two dashed lines, representing the frequency difference. A small number '7' is visible in the top right corner of the plot area.
$M\text{funfreq}$	A mean frequency (Hz) of a fundamental frequency	 A spectrogram showing frequency content over time. A single horizontal dashed red line is drawn across the plot, indicating the mean frequency of a fundamental frequency. A small number '7' is visible in the top right corner of the plot area.

Δ_{domfreq}	A difference between minimum and maximum frequency (Hz) of a dominant frequency	
M_{domfreq}	A mean frequency (Hz) of a dominant frequency	
T_{domfreq}	A time duration (s) of a dominant frequency	
$\Delta_{\text{inimaxdomfreq}}$	A difference between initial and maximum frequency (Hz) of a dominant frequency	

$\Delta \text{maxfindomfreq}$	A difference between maximum and final frequency (Hz) of a dominant frequency	
$T_{\text{maxfindomfreq}}$	A duration in time from maximum frequency to final frequency (s) of a dominant frequency	
$T_{\text{iniflucdomfreq}}$	A duration in time from initial frequency to the first fluctuation point (s) of a dominant frequency	
$T_{\text{inimaxdomfreq}}$	A duration in time from initial frequency to maximum frequency (s) of a dominant frequency	