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Influence of snow, food, and rock cover on Royle's pika abundance in western Himalaya

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Abstract

Knowledge on demographic responses to environmental and microhabitat factors are crucial to understand the ecological consequences of climate change predictions for species that live in isolated mountainous habitat, such as the Royle's pika. We examined the influence of snow attributes, food availability, and rock cover on adult and juvenile pika counts and juvenile emergence date based on spatiotemporal variation in these parameters at 10 permanent plots (0.25 ha squares) along an attitudinal gradient of Kedarnath Wildlife Sanctuary during the predispersal period spanning four years. Pika count and its interannual variability at plots were estimated at $4.06_{\text{Mean}} \pm 0.21_{\text{SE}}$ and 19.65 ± 1.71% $\overline{CV}$ respectively. Regression analysis showed that spatiotemporal variation in adult counts was related to the interactive effect of snow-cover period and altitude wherein counts increased with snow-cover period only in lower altitudes ($\beta = 0.26 \pm 0.08$). Juvenile count was related to spring snow-depth ($\beta = 0.074 \pm 0.037$). Litter number was typically one. Our results confirm the influence of snow as thermal insulator (to pika and their food plants) on population dynamics of small mammals. We also highlight that adult and juvenile populations might be governed by different factors, invoking further studies on age-stratified assessment of population responses to climate change.

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Introduction

Fluctuating environmental conditions can influence the evolution and life history of a species, and short-term fluctuations in particular can directly affect population dynamics (Boyce, 1988; Yoccoz and Ims, 1999). The majority of cold regions experience marked seasonality, characterized by a short vegetation growing period during summer and a prolonged winter with considerable snow cover. But in contrast to high latitudes, climate at high altitudes also exhibit marked diel variability (Barry, 1992). Additionally, the magnitude of climate change is higher in alpine regions than in lower altitudes (Naftz et al., 2002). Alpine species that are adapted to cold climates, live in highly fragmented and isolated mountain habitat, and have poor dispersal abilities, might be especially vulnerable to climate change, because they may not be able to move their ranges and adapt quickly enough to track shifts in suitable microclimate or habitat that result from a rapidly changing climate (Hughes, 2000; Moritz et al., 2008; Schloss et al., 2012). Therefore, significant change in montane climatic conditions may lead to the extirpation of alpine species with low adaptive capacity and narrow bioclimatic niches (Beever et al., 2003, 2010).

Pikas (*Ochotona* spp.) are small, herbivorous lagomorphs found in alpine ecosystems, where they play important functional roles (Smith and Foggin, 1999). They strongly influence the composition of local plant community through ecological engineering that leads to increased plant diversity (Bagchi et al., 2006). They are an important prey for many endangered small carnivores (Roberts, 1977; Oli et al., 1994) and have positive impacts on soil nutrients and moisture gradients, thereby benefiting several birds and mammals (Smith et al., 1990). Pikas, especially the talus-dwelling species, have several traits that make them vulnerable to climate change. This includes poor dispersal ability, close association with patchy habitats on mountain islands, high sensitivity to temperature fluctuation, and low fecundity (Smith and Weston, 1990; Beever et al., 2010). Recent studies (Beever et al., 2003, 2010; Calkins, 2012) indicate that pika distribution and abundance in the United States is strongly governed by climatic drivers. In the western part of the continents, pika distribution has shifted 153 m uphill over the course of several decades (~17 m per decade over ~90 years; Moritz et al., 2008). While Rodhouse et al. (2010) indicated that talus-dwelling pika distribution is significantly affected by their habitat topography and microclimate (bioclimatic niche), Southwick et al. (1986) showed that their populations are remarkably stable in spite of high variability in alpine precipitation. More recently, some low elevation pika populations have been reported to persist outside the limits of their previously known bioclimatic niche (Simpson, 2009). Thus, pikas' response to climate change are rather complex and can vary significantly among different locations. Hence, understanding species-specific responses to changing climate is extremely important not only for identifying the mechanisms involved, but also for developing effective monitoring, management, and conservation strategies (Stenseth et al., 2002; Hallett et al., 2004).

Although Himalaya is home to seven different pika species, the absence of long-term data on these species prevents any sort of projection analysis of their responses to future climate change (Smith et al., 1990). Royle's pika (*Ochotona roylei*) is one of the most widely distributed but least studied alpine lagomorphs of Himalaya. The species (typically 100–150 g in weight; Alfred et al., 2006) inhabits talus landscapes and is distributed throughout northwestern Pakistan, India, Nepal, and the adjacent region on the Tibetan Plateau. It inhabits rocky slopes between 2400 m and 5000 m above sea level (Smith et al., 1990; Chakraborty et al., 2005). Previous studies on Royle's pika focused on their behavior and were short-term (Kawamichi, 1968, 1971). Unlike other talus dwelling pikas, Royle's pika does not show prominent hoarding behavior (Kawamichi, 1968, 1971; Smith et al., 1990; Bhattachar-

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yya et al., 2013). These animals are diurnal and easily visible, making them ideal for field observation (Beever et al., 2010).

In this study, our objectives were (1) to estimate basic population parameters like abundance, litter number, and juvenile emergence time; and (2) to determine the influence of environmental factors on abundance of juvenile and adult Royle's pika. While our short-term study (Bhattacharyya et al., 2009) has indicated that their abundance is influenced by rock cover, here we examine the effects of snow attributes, food availability, and rock cover on their abundance. Climate change might increase winter temperature, which could result in early snow melt as well as increase alpine soil dryness, reduce soil nitrogen availability, and alter growth and availability of alpine plants (Walker et al., 1994, 1995; Brooks and Williams, 1999). Following earlier studies (Bunnell and Johnson, 1974; Smith and Ivins, 1983; Kreuzer and Huntly, 2003; Franken and Hik, 2004; Morrison and Hik, 2007) on other talus-dwelling pikas such as the American pika (*O. princeps*) and collared pika (*Ochotona collaris*), we made the following predictions. We monitored populations for four years in 10 permanently marked plots, and tested these a priori ecological predictions through a set of competing regression models in an information theoretic framework.

PREDICTIONS—INFLUENCE OF SNOW ATTRIBUTES ON ADULT PIKA

Snow cover and depth provide thermal insulation from extreme temperature fluctuations during winter (critical period) to adult pika and their food plants, thereby increasing the survival of both (Marchand, 1996; Franken and Hik, 2004; Morrison and Hik, 2007). Hence, we predict that (a) snow-cover period and mean snow-depth will positively influence adult abundance. Since general climatic conditions differ significantly between altitudes and can change the impact of snow, we also expect (b) an interactive effect of altitudinal zone and snow-cover period and mean snow depth on adult abundance (e.g., short snow-cover period at lower altitude due to warmer climate might have higher negative influence, or more adult pika abundance, than in higher altitude).

INFLUENCE OF SPRING SNOW DEPTH, FOOD AVAILABILITY, AND ROCK COVER ON JUVENILE PIKA

(c) Since adult females breed around springtime (Smith et al., 1990), spring snow-depth will reduce cold stress to pregnant females (Kreuzer and Huntly, 2003; Franken and Hik, 2004; Morrison and Hik, 2007), and hence thick snow depth will favor (positive influence) juvenile abundance. (d) Pika spend 42% of their activity budget in feeding (Bhattacharyya, unpublished results), and energetic demands are higher for juveniles, as smaller size raises metabolic requirement, and lactating females. Hence, food availability will positively influence juvenile abundance. (e) Furthermore, juveniles spend considerable time in locomotion (>70%) compared to adults (22%; Bhattacharyya, unpublished results), which makes them more vulnerable to predation risk. Therefore, high amount of rock cover may also benefit juvenile abundance by providing escape cover (Roach et al., 2001).

Methodology

STUDY AREA

The study was performed within a 4 km^2 region (Chopta to Tungnath, coordinates: 30°30′–31°29′N and 78°12′–79°13′E) in the Kedarnath Wildlife Sanctuary (~975 km^2) which is located in the upper catchment of the Alaknanda River in Chamoli District, Uttarakhand. The elevation ranged from 2900 m to 3680 m a.s.l. (subalpine to alpine). Local climate was influenced by the southwest monsoon (rainy season) in summer and westerly disturbances in winter (Mani, 1981). The area had five seasons: spring (March to April), summer (May to June), monsoon (June to September), autumn (October to November), and winter (December to February) (Table 1; Adhikari et al. 2011). Major precipitation fell from the end of June until mid-September (Table 1; Adhikari et al., 2011).

The vegetation in the subalpine region mostly comprised broad-leaved sclerophyllous stands of *Quercus semecarpifolia, Rhododendron arboreum*, *R. campanulatum*, *Abies pindrow*, *A. spectabilis,* and *Sorbus* sp., whereas the alpine meadows at and around Tungnath were dominated by diverse grasses and herbaceous plants (Sundriyal et al., 1987). Some of the potential predators of pikas in the study area were jackal (*Canis aureus*), red fox (*Vulpes vulpes*), yellow-throated marten (*Martes flavigula*), Himalayan weasel (*Mustela sibirica*), and common leopard (*Panthera pardus*) (Green, 1985).

ESTIMATION OF PIKA ABUNDANCE

We recorded the abundance of Royle's pika in 10 permanently marked plots (50 × 50 m^2) along a 780 m altitudinal gradient starting from 2900 m a.s.l. Plots were grouped into two altitudinal zones: alpine (3300–3680 m, n = 5) and timberline-subalpine (2900–3300 m, n = 5). Each plot was surveyed for pika once in a month during the predispersal period (May–August) from 2008 to 2011 (except for July–August 2010 and May 2011), yielding a total

TABLE 1

Summary of mean temperature and precipitation range during different seasons in the study area.

Season	Mean air temperature range (°C)	Mean precipitation range (mm)
Spring	1.2 ± 0.2 to 6.2 ± 0.3	13.6 ± 6.7 to 22.2 ± 7.9
Summer	6.7 ± 1.0 to 11.3 ± 1.2	90.9 ± 23.1 to 363.6 ± 105.0
Monsoon	10.9 ± 1.0 to 13.6 ± 1.1	461.6 ± 67.9 to 715.6 ± 52.7
Autumn	4.8 ± 0.2 to 10.8 ± 1.0	12.4 ± 3.5 to 19.6 ± 8.5
Winter	–1.0 ± 0.2 to 4.3 ± 0.3	43.6 ± 6.5 to 48.12 ± 10.6

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of 390 sampling occasions. On each occasion, we conducted three sessions of 4 hours' duration in each plot (morning: 06:00–10:00; day: 10:00–14:00; evening: 14:00–18:00 hours). Royle's pika was classified into two distinct age groups—juvenile and adult—which could be distinguished based on morphological features such as body size, coat color, pattern of molting marks, and scar marks on the ears (Bhattacharyya et al., 2009). Juvenile Royle's pikas were found to be significantly smaller than adult pikas with no molting marks throughout the predispersal periods. Unlike North American pikas, juvenile Royle's pikas emerge from natal sites in May and remain at natal sites until the end of August (Bhattacharyya's unpublished data). Therefore, we successfully identified individuals for abundance estimation using morphological features (mentioned above), activity location, and photo documentation. Royle's pika habitats in alpine zone were rocky and scrub meadows, rubble wall, broken slope, and *Danthonia* grassland; whereas, habitats in timberline-subalpine zone were mixed herbaceous meadow, rocky and broken slopes, rocky forest edge, and boulder-strewn forest gap. Rock cover was highest (72%) in the subalpine broken slope and least (10%) in mixed herbaceous meadows.

An index of pika abundance was calculated by taking the average individual count for three observation sessions in one day and then merging them to obtain monthly and annual estimates (Bhattacharyya et al., 2009). We estimated plot and survey detection probabilities following Bhattacharyya et al. (2009). Detection probabilities of pikas across plots were regressed against various habitat variables such as food availability, rock cover, altitudinal zone, and herbaceous plant species richness. We found that detection probability was only influenced by herbaceous species richness, and that too weakly ($R^2 = 0.23$, $P < 0.01$). Hence, we assumed that imperfect detection probabilities would not confound the actual effects of other habitat variables (food availability, rock cover, or altitudinal zone) as evidenced by the abundance index.

In each plot, we recorded the percentage rock cover visually. We identified pika food plants by focal sampling (Altmann, 1974) and found that they forage on 26 different plant species in this area (Bhattacharyya et al., 2009). We used a standard quadrat method (Rawat and Adhikari, 2005) to estimate the density of these food plants. Ten 1 × 1 m quadrants were deployed randomly within each permanent plot at monthly intervals. The availability of food plants (individuals m^{-2}) in a study plot was calculated after pooling the abundances of all food plants for that plot. We recorded snow depth at 10 fixed points in each plot on a monthly basis during winter and spring over four years (2007–2011). We pooled the data to estimate the average annual snow depth and average spring snow depth. The snow cover period was defined as the number of days in which at least 5 of 10 snow-depth measuring points in a study plot were covered by snow. The day of first juvenile pika sighting in a plot was used as an index of juvenile emergence time.

Data Analysis

We tested if the covariates were normally distributed using Kolmogorov-Smirnov test, and, whenever necessary, applied square root transformation to achieve normality (Zar, 1999). Adult population data were log-transformed before regression analyses. To avoid multicollinearity among covariates, we conducted Pearson's correlation analysis and considered predictor variables with Pearson's correlation coefficient (r) > 0.4 as highly correlated (Quinn and Keough, 2002). We found cross-correlation between the potential covariates of pika abundance. Food availability had a weak but significant correlation with annual snow depth ($r = 0.235$, $p < 0.05$) and snow cover period ($r = 0.291$, $p < 0.05$). All snow attributes were correlated with one another (snow-cover period and spring snow depth: $r = 0.408$, $p < 0.001$; snow-cover period and annual mean snow depth: $r = 0.899$, $p < 0.001$; spring snow depth and annual mean snow depth: $r = 0.419$, $p < 0.001$) and with altitudinal zone (spring snow depth: $r = 0.536$, $p < 0.001$; annual mean snow depth: $r = 0.607$, $p < 0.001$, snow-cover period: $r = 0.514$, $p < 0.001$). Therefore, these variables were not included in the same model unless specified as an interaction term with altitudinal zone.

We began our analyses by identifying if the interannual variation in pika population corresponded with that of any environmental parameter. For this, we used linear mixed models, where we treated juvenile and adult pika abundances, snow-cover period, annual snow depth, spring snow depth, and food availability as separate response variables, and years as an explanatory variable, controlling for the random difference between plots. Year was considered as a dummy covariate, where effects of 2009–2011 were tested against 2008. Following Zuur et al. (2009), we built models by Laplace approximation and restricted maximum likelihood parameter estimation using "lmer" function of lme4 package in program R (http://www.rproject.org/).

Thereafter, we directly tested the response of pika abundance to potential covariates using linear regression analysis on the covariation of these parameters across plots and years. To test our predictions (mentioned in the Introduction), we constructed a set of regression models incorporating additive and interactive effects of one or more of the following covariates: snow-cover period, annual mean snow depth, spring snow depth, food availability, and rock cover. In total, we compared six models explaining adult pika abundance and five models for juvenile abundance over the null model that assumed constant abundance across space and time (Table 2). Following Burnham and Anderson (2002), we either selected the best candidate model if its AICc value was >2 units than the competing models, otherwise we used multimodel averaging. Our data were nested within plots and years, which could introduce dependence between observations and violate assumptions of regression analysis (Zar, 1999). We examined this possibility by building generalized linear mixed effect models (GLMM) with plot as random intercept, but observed nonsignificant random variation around the intercept, indicating that there was no such grouping of observations (Zuur et al., 2009). Hence, we followed the conventional linear model routine for the above analysis. To identify factors correlated with the emergence of juvenile pika at each site, emergence date was modeled on snow cover period, spring snow depth, food availability of emergence-month, and altitudinal zone following similar statistical approach as described above.

Results

Pika abundance-index (mean total count in a 4-h occasion in a plot) was estimated at 4.05 ± 0.20 individuals per site, that is, a density of 16.23 ha^{-1}. Pika count and its interannual variability at plots were estimated at $4.06_{Mean} \pm 0.21_{SE}$ and 19.65 ± 1.71% $\overline{CV}$, respectively. Overall abundance index was generally lower in timberline through subalpine boulder-strewn forest gaps ($2.03_{mean} \pm 0.20_{SE}$) and *Danthonia* grassland habitat (2.47 ± 0.31) than other plots (4.51 ± 0.18; Fig. 1). Adult females gave birth to only one litter per year. Adults and juveniles were significantly less in 2009 than 2008 (Table 2). Our analyses indicated that pika abundance was higher in years (e.g., winter of 2010–2011) with deeper snow (59.59 ± 4.48 cm), longer snow cover period (111.9 ± 4.5 days), and high food availability (503.0 ± 14.43 plants m^{-2}). This result

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TABLE 2

Summary statistics for linear mixed effects models testing for significant interannual variations (2008 vs. 2009, 2010, 2011) in adult and juvenile pika population abundances, snow cover period, annual mean snow depth, spring snow depth, and food availability at the study area (n = 10).

Parameters		Beta	SE	t-value
Adult abundance	Intercept	2.87	0.16	17.21
	Year 2009	–0.58	0.21	–2.66*
	Year 2010	0.04	0.24	0.20
	Year 2011	–0.29	0.24	–1.20
Juvenile abundance	Intercept	1.57	0.18	8.40
	Year 2009	–0.41	0.19	–2.09*
	Year 2010	0.12	0.21	0.57
	Year 2011	–0.20	0.21	–0.94
Snow cover period	Intercept	95.80	3.93	24.34
	Year 2009	–24.80	0.68	–36.05*
	Year 2010	0.10	0.76	0.13
	Year 2011	16.10	0.76	20.93*
Annual mean snow depth	Intercept	35.46	4.70	7.54
	Year 2009	–12.28	0.92	–13.30*
	Year 2010	–6.06	1.03	–5.88*
	Year 2011	24.13	1.03	23.37*
Spring snow depth	Intercept	44.18	3.68	12.02
	Year 2009	–20.65	1.23	–16.78*
	Year 2010	–25.68	1.37	–18.66*
	Year 2011	–25.85	1.37	–18.79*
Food availability	Intercept	258.74	46.67	5.54
	Year 2009	–44.63	39.35	–1.13
	Year 2010	76.60	44.00	1.74
	Year 2011	244.27	44.00	5.55*

*Indicates statistically significant change ($p < 0.05$).

was congruent with our predictions that snow melting pattern and food availability influence Royle's pika abundance.

For adult pika abundance (Table 3), a model incorporating interactive effect of snow-cover period and altitudinal zone received more support than the null model (ΔAICc = 7.10) and other competing models (ΔAICc > 2). This model showed that snow-cover period or altitude per se did not influence adult abundance, but snow-cover period positively influenced adult abundance in the timberline-subalpine zone compared to alpine zone (Table 4). This result indicated differential influence of altitude on the relationship between snow cover period and adult pika abundance, which was consistent with our second prediction. For juvenile pika abundance, two models incorporating food availability, rock cover, and spring snow depth received more support than other models (ΔAICc > 2, Table 3). Food availability and spring snow depth showed significant positive influence on juvenile abundance, which was consistent with our third and fourth prediction, which indicated importance of spring snow depth and food availability for juvenile pikas (Table 4). We did not get strong support for our final prediction, as the influence of rock cover on abundance of juvenile pika was less precise (Table 4). The regression result (Table 4) predicted that 38 days (2 standard deviation) increase in snow cover period will also increase (64%) adult pika relative abundance in lower altitude, whereas only little (11%) increase in high altitude adult relative abundance will be observed. Similarly, in case of juvenile pika, regression result predicted that 32cm (2 standard deviation) increase in spring snow depth will show minor increase (12%) in juvenile relative abundance.

Broadly, juvenile pikas were encountered earlier (4.13 days) in the timberline-subalpine zone than in alpine zone (Fig. 2). The earliest emergence of juvenile pika occurred on timberline-subalpine broken slopes and boulder-strewn forest gaps (8 May 2010). The latest emergence (8 June 2009) occurred in alpine rocky and scrub meadows. The best model explaining juvenile pika emergence pattern incorporated an interactive effect of snow-cover period and altitudinal zone, and was more informative than the null model (ΔAICc = 204.85) and other models (ΔAICc > 2). The standard deviation for random effects of site was 4.66, indicating that there was considerable variation in emergence time between plots through years. This model showed that a short snow-cover period delayed juvenile emergence date ($\beta = -0.337 \pm 0.11$, t = 2.96) and a less precise interaction effect of altitude on snow-cover period ($\beta = -0.103 \pm 0.073$, t = 1.41).

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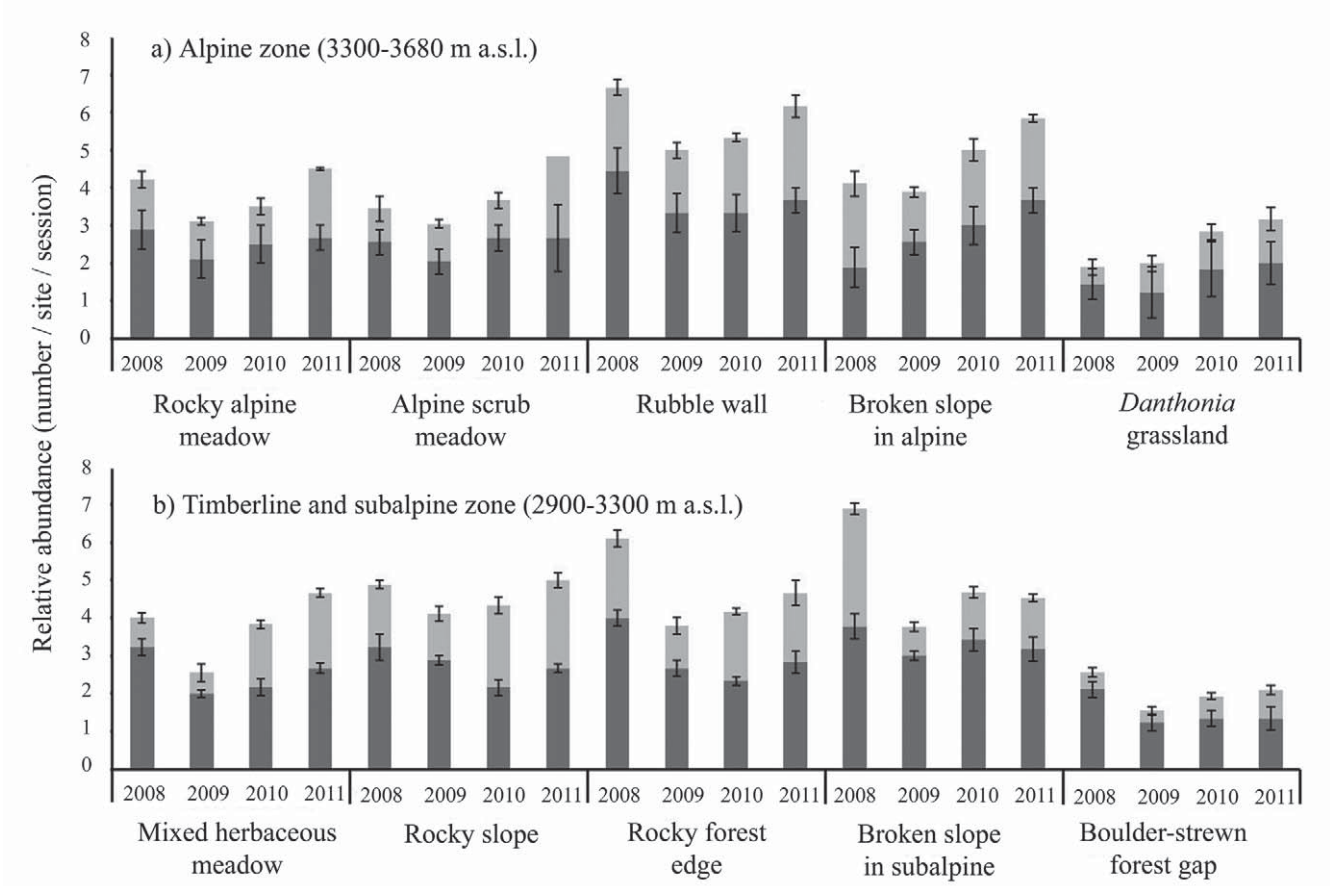


FIGURE 1. Relative abundance of Royle's pika in different habitat types of the alpine and timberline-subalpine zones during the predispersal period (May-August) from 2008 to 2011 (except for July–August 2010 and May 2011); light colored bars represent juvenile pika and dark colored bars represent adult pika abundance. Values are means ± S.E.

Discussion

In this study, pika abundance was significantly affected by climatic (snow melting patterns) and habitat (rock cover, food availability) characteristics. Thick snow cover acts as a protective insulation layer for pikas during winter, allowing them to survive large diel temperature fluctuations during winter and early spring (Morrison and Hik, 2007). Royle's pika does not hibernate in winter and does not construct hay-piles for winter food (Kawamichi, 1968; Bhattacharyya's unpublished data). Thus, adult pikas face harsh climatic conditions during winter (in contrast to juvenile pikas, which are usually born in early summer). This explains why snow attributes were more important explanatory factors for abundance of adult pikas than other habitat characteristics, such as amount of rock cover or food availability. During the winter of 2009, the short snow cover period may have increased adult pika mortality due to cold stress, in turn resulting in low pika abundance the following summer. Kreuzer and Huntly (2003) found that snow melting pattern and its duration has a significant impact on the demography of the American pika. Acute cold stress (due to a short period of snow cover or a thin snowpack) is also an important cause of American pika extirpation in the Great Basin region of the southwestern U.S.A. (Beever et al., 2010). The thermal insulation provided by a thick snowpack reduces cold stress and thermoregulatory energy demands by creating a favorable environment for successful reproduction in adult pika, thereby positively influencing juvenile pika abundance. Snow distribution in the alpine environment is often governed by the interaction of wind and topography; while snow generally falls evenly, strong winds usually remove snow from ridges and deposit it in drifts and other sheltered places. This variation in snow cover duration, as well as depth across plots or years, may have contributed to the intra- and intersite variation in the abundance of adult and juvenile pika that we observed.

Winter snow cover also works as a thermal insulation for vegetation, protecting alpine plants from extreme cold and fluctuating temperatures (Marchand, 1996). Snow cover period and depth are critical influences on soil nutrient quality and thus have a profound effect on alpine food plant growth (Walker et al., 1994, 1995; Brooks and Williams, 1999). Although alpine soils are frozen and snow-covered for much of the year, soil particles are reportedly surrounded by water films, even at –10°C (Romanovsky and Osterkamp, 2000), allowing microbial activity to continue in winter (Coxson and Parkinson, 1987; Rivkina et al., 2000; Mikan et al., 2002). Therefore, deep snow during winter and early spring may alter the soil microbial community by increasing their nutrient pool as well as that subsequently available to plants in the following growth season (Buckeridge and Grogan, 2008). In alpine and tundra ecosystems, soil nitrogen supply is limiting; thus, a change in nitrogen supply can significantly influence phenology and biomass of alpine plants (Shaver and Kummerow, 1992; Schimel et al., 1996). Thick snow cover results in later snowmelt, which delays the beginning of the

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TABLE 3

Relative support for various candidate models testing competing ecological postulates. The postulates are for factors affecting abundance of Royle's pika using information theoretic criteria for different study plots (n = 10; AICc values = Akaike's information criterion, Log(L) = likelihood, K = number of modeled parameters, ΔAICc = the difference between the model indicated and the best model [the model with lowest AICc], and Wi = Akaike weights).

Model (predictor)	–2 × Log(L)	K	AICc	ΔAICc	*Wi*
Adult pika abundance					
Snow cover period × altitudinal zone	–35.97	3	81.95	0.00	0.90
Annual mean snow depth × altitudinal zone	–38.38	3	86.76	4.80	
Snow cover period	–40.71	3	87.42	5.46	
Rock cover + Snow cover period	–39.97	4	87.95	5.99	
Null model	–42.52	2	89.05	7.10	
Food availability	–42.11	3	90.22	8.26	
Rock cover	–42.14	3	90.29	8.33	
Juvenile pika abundance					
Food availability + spring snow depth	–40.02	4	88.04	0.00	0.39
Rock cover + spring snow depth	–40.19	4	88.39	0.34	0.33
Null model	–42.52	2	89.05	1.01	0.28
Food availability	–42.11	3	90.22	2.17	
Rock cover	–42.14	3	90.29	2.24	
Food availability × altitude zone	–42.46	3	92.93	4.88	

growth season and reduces frost mortality in herbaceous plant buds (Inouye, 2008). These observations are congruent with the findings of our study, which indicate that a protracted snow cover period and thick snow pack result in high availability of food plants. This effect may improve pika health by increasing nutritional intake during the breeding season in spring and during the remainder of the summer.

Seasonality and duration of growing periods are considered to be principal factors governing annual litter size of long-lived herbivorous small mammals such as pikas in alpine ecosystems (Smith and Ivins, 1983). In this present study, Royle's pika was found to have one litter annually, even the year with low juvenile abundance, whereas similar talus-dwelling pika, such as the American pika, are reported to have two litters per year if they lose the first litter due to high predation or extreme winter condition (Smith and Ivins, 1983). Low availability of food resources (no winter hay-pile) and high energy demands due to thermoregulatory mechanisms for surviving in extremely variable climate may explain the reduced frequency of reproduction in Royle's pika. In both collared

TABLE 4

Estimated influences of parameters (snow cover period, spring snow depth, food availability, rock cover, and altitudinal zone) on adult and juvenile Royle's pika abundance measured by the best fit general linear model (minimum Akaike information criterion).

Parameter	Beta-values	SE
For adult		
Intercept	0.85	0.05
Snow cover period	–0.05	0.05
Altitudinal zone	–0.01	0.08
Snow covered period × altitude zone	0.25	0.08
For juvenile		
Intercept	0.91	0.04
Food availability	0.05	0.04
Rock cover	0.04	0.04
Spring snow depth	0.07	0.04

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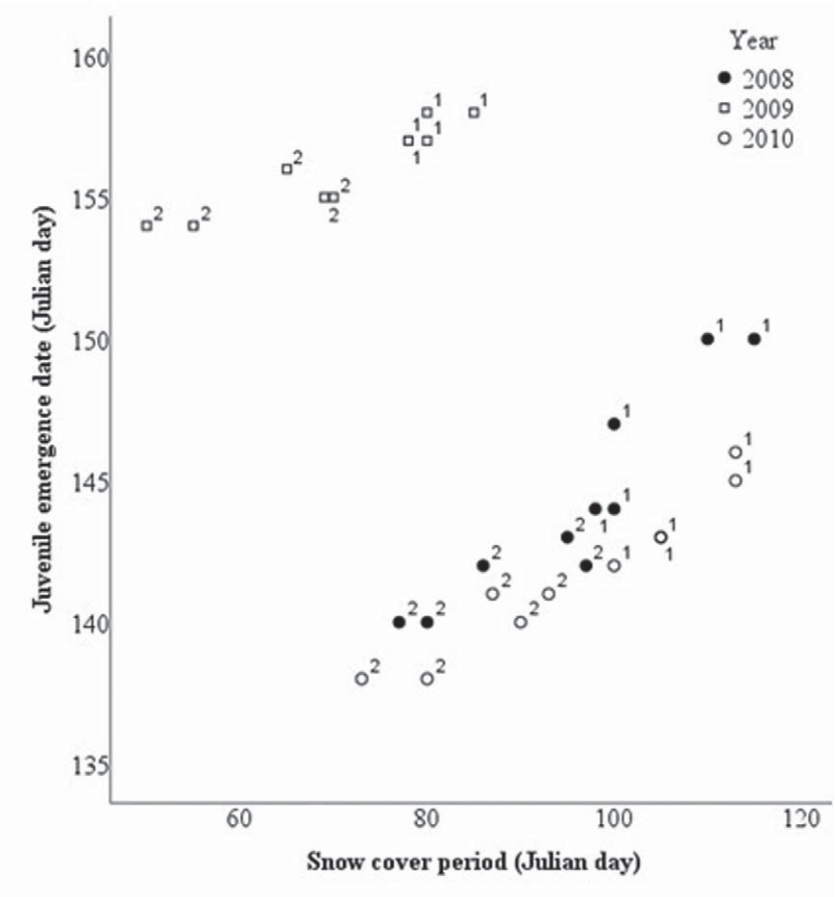


FIGURE 2. Influence of snow cover period on emergence time of juvenile Royle's pika (1 = alpine zone, 2 = timberline-subalpine zone).

and American pika, the timing of parturition is influenced by variation in snow melt and the start of the vegetation growth period (Millar and Zwickel, 1972; Smith, 1978). In Royle's pika, juvenile emergence timing was delayed by thin snow cover and early snow melt, which reduces the growth of alpine vegetation (Walker et al., 1994, 1995). Therefore, Royle's pika females likely delay breeding to ensure optimization of the sole reproductive opportunity in the year, thereby reducing fetus mortality due to large postwinter weather fluctuations and also ensuring the availability of plentiful food resources during lactation and the only chance to successfully wean litters in the year (Morton and Sherman, 1978). These observations likely explain why juvenile pika appearance at lower altitude was delayed by 10–15 days in 2009 when snow melted ca. 20–25 days earlier than in other years.

Pikas venture out from their burrows to forage and return back after each feeding bout (Orians and Pearson, 1979; Roach et al., 2001). Therefore, loss to predation is an important cost associated with each foraging bout. To minimize predation while maximizing available forage, pikas take advantage of rock cover. This was demonstrated in the present study, which identified rock cover as an important factor governing juvenile pika abundance. These results are also congruent with earlier research on American pika that suggested a positive linear relationship between pika abundance and talus rock size (Bunnell and Johnson, 1974). The amount of rock cover in the habitat also has significant influence on the seasonal abundance of Royle's pika in the western Himalaya (Bhattacharyya et al., 2009).

We have revealed basic relationships between Royle's pika abundance and the environmental factors. Pikas were reported to be extremely philopatric in nature (Smith and Ivins, 1983), and the probability of moving across highly fragmented and isolated rock talus is often very low. Additionally, Royle's pika need to have crevices for living in, as they can't make burrows, and not all rock talus necessarily has suitable crevices (Smith et al., 1990). Hence, it will be unlikely that pikas will be moved large distances to reach favorable parts of mountain in harsher years. During the study period, no pika population migration along altitude gradient or across habitat were observed. Therefore, the environmental conditions directly influence pika abundance in the study area. This study also indicated that different age class within a population might be affected differently by changes in environment. This invokes the need of age-specific assessments and monitoring of climatic variability on small mammal population performance. Shrestha et al. (2012) found that Himalaya has been warmed by 1.5 °C (1982–2006) with the greatest increase (1.75 °C) in winter temperature rather than any other season. There is an increased trend in summer precipitation, but winter precipitation was found to be significantly decreased in Himalaya (Shrestha et al., 2012). As Royle's pika does not show prominent hoarding behavior, decreasing winter precipitation might cause more cold stress, increase energy demand in a food-scarce environment, and negatively influence the abundance. Therefore, long-term studies on influence of climate on Royle's pika abundance can reveal the possibility of using them as indicator species to track and quantify effects of climate change in the alpine Himalaya.

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APPENDIX

Table A1

Average detection probability of Royle's pika in various habitat types during observation sessions.

Habitat types	Average detection probability
Rocky alpine meadow	0.636
Alpine scrub meadow	0.619
Rubble wall	0.731
Broken slope	0.678
Danthonia grassland	0.590
Mixed herbaceous meadow	0.731
Rocky slope	0.753
Rocky forest edge	0.654
Broken slope	0.601
Bouldery forest gap	0.550

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