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American pikas' (*Ochotona princeps*) foraging response to hikers and sensitivity to heat in an alpine environment

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Abstract

Optimal foraging theory predicts tradeoffs in animals balancing net energy intake and predator avoidance. In particular, overall foraging activity could be low if (1) perception of predation risk is high or (2) abiotic conditions are suboptimal. American pikas (*Ochotona princeps*) are small, food-hoarding mammals whose foraging opportunities are restricted by heat and risk of predation. If hiking disturbance is perceived by pikas as predation risk, it could reduce the amount of food stored overwinter, possibly affecting survival. We simulated hiker disturbance events for 48 pikas in Mount Revelstoke and Glacier National Parks, British Columbia, to estimate foraging time lost due to hikers. We tested risk avoidance hypotheses using four indicators of risk behavior: alert distance (D_A), flight initiation distance (D_F), exit delay (T_E), and delay in return to forage (T_R). All hiker disturbance events elicited antipredator behaviors in foraging pikas and reduced foraging time; however, when compared to increasing temperatures over 4–6 hour observation periods, the latter best predicted a reduction in pikas' foraging activity. For every 1 °C increase in temperature, pika foraging activity decreased by 3%. Pikas near trails (<50 m) lost an average of 4.1 (SE = 0.6) minutes of foraging time per disturbance event compared to 13.2 (SE = 1.7) minutes lost by pikas with territories >100 m away from trails. Such differences might reflect habituation in pikas undergoing frequent disturbance. Monitoring pika populations for declines would be sensible given projected trends in warming climate and potential increases in hiking traffic.

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Introduction

Alpine habitats host unique animal diversity and often are sensitive to disturbance (Korner and Spehn, 2002; Willard et al., 2007). Human recreation areas and trail networks are found within many mountain parks and introduce novel disturbances to the alpine environment (Leung and Marion, 2000; Frid and Dill, 2002; Griffin et al., 2007). While hikers rarely harm alpine animals directly, non-lethal disturbance can affect animal behavior, foraging, and energy budgets, suggesting that indirect effects of hiking traffic might be important to consider in the conservation of alpine species (Lima, 1998; Frid and Dill, 2002; Sirot, 2010). Alpine and tundra habitats are generally assumed to be undisturbed by human influence given their remote setting; however, by the late 1970s, 12% of tundra ecosystems in the western United States were found to be impacted by historical or current anthropogenic activity or development (Brown et al., 1978). Further, these habitats are experiencing altered precipitation and temperature regimes (ACIA, 2005). Changes in plant communities associated with climate change, such as shrub encroachment on alpine and tundra ecosystems, could decrease habitat available to pikas (Myers-Smith, 2011).

American pikas (*Ochotona princeps*) are small mammals that reside primarily in the alpine zone. During the brief snow-free season, pikas forage in exposed meadows, increasing their exposure to predation (Millar and Zwickel, 1972; Smith, 1974; Huntly et al., 1986). When foraging, pikas are either grazing for immediate sustenance or stockpiling vegetation in a central location (haystack) for winter consumption (Barash, 1973; Dearing, 1997). Unlike many small mammals in the alpine, pikas stay active year-round and do not hibernate, relying on their central food cache to overwinter (Dearing, 1997). Pikas received considerable attention following

documented extirpations of some low elevation populations in the Great Basin (Beever et al., 2003; Wilkening et al., 2011). Global climate change has been implicated as a driver of population declines, although human disturbance could not be ruled out (Beever et al., 2003, 2010; Wilkening et al., 2011). Distance from the nearest road was found to be a significant factor in predictive models describing pika population persistence; the farther from a primary road, the less likely the population was to be extirpated (Beever et al., 2003). Though pikas' thermal limitations are documented, their vulnerability to hiker disturbance and its relative importance for pika population persistence is not well understood.

Pikas may perceive humans as predators (Frid and Dill, 2002). Optimal foraging theory predicts that animals manage risk responses by balancing energetic requirements with perceived exposure to predation (MacArthur and Pianka, 1966; Lima and Dill, 1990). If true, optimal foraging theory suggests that pikas could change foraging behavior to increase vigilance and other antipredator behaviors in the presence of hikers at a cost of stockpiling food (MacArthur and Pianka, 1966; Lima and Dill, 1990).

Pikas depend, in part, on accumulated food stores for survival over long (9–10 month) winters, in which they do not hibernate but remain metabolically active beneath the snow (Millar and Zwickel, 1972; Smith, 1974; Dearing, 1997; Morrison and Hik, 2007). In the summer foraging season, pikas are extremely sensitive to heat and are unable to thermoregulate when exposed to temperatures higher than 25 °C (MacArthur and Wang, 1973; Smith, 1974). Warm temperatures can restrict pikas to their cooler, talus-based territories and limit pikas' ability to forage (Smith, 1974). In this context, human disturbance and pikas' perception of risk associated with hiking groups could jointly limit time available to collect food beyond expectations based only on climate implications for food hoarding and overwinter survival.

We used predation risk theory to evaluate the effects of human disturbance and warm days on pika foraging behavior in an alpine habitat. Predation risk theory suggests that antipredator behavior can be influenced by three general categories of behavioral predictors: characteristics of the predator, characteristics of the prey, and environmental factors such as temperature (Lima and Dill, 1990; Frid and Dill, 2002). Characteristics of the predator, in the case of hikers, include attributes such as whether the hiker is approaching the pika directly, or passing at a tangent. Characteristics of the prey include the position of the prey, such as the individual's proximity to hiking traffic. We tested hypotheses about how factors in these attribute categories might affect pika response to hikers, and we selected attributes that might be relevant to the design and management of trail networks and hikers' behavior. We also tested the hypothesis that warm temperatures and pikas' response to human disturbance costs the pikas foraging time.

Methods

STUDY SYSTEM

Ochotona princeps is a small lagomorph that lives in alpine regions of mountainous areas from the Great Basin in the United States to northern British Columbia, Canada. Their habitat mainly consists of rocky boulder fields (talus slopes) in subalpine and alpine zones, although there are populations that persist at lower elevations (Beever et al., 2008; Simpson, 2009). Boulder fields provide protection from predators and serve as a refuge from warmer daytime temperatures (Smith, 1974; Holmes, 1991). Pikas are diurnal, territorial, central-place foragers that stockpile food in one or several haypiles (Millar and Zwickel, 1972; Dearing, 1997). Individuals defend haypiles and rarely forage more than 10 m from the talus (Barash, 1973; Morrison et al., 2004; McIntire and Hik, 2005).

We studied pika populations in the Columbia Mountains of British Columbia, Canada, at three sites in Mount Revelstoke and Glacier National Parks. The sites in Glacier National Park were located near Avalanche Crest trail (51°16'16"N; 117°28'45"W) and Abbott Ridge trail (51°15'00"N; 117°28'45"W). The site in Mount Revelstoke National Park was located near the Eva Lake trail (51°03'52"N; 118°06'42"W). We set up infrared trail counters 1.3 m off the ground next to trails leading to each of our field sites from 1 August to 30 September 2012 to record the number of hiking groups that pikas near trails encountered. We defined a hiking group as any number of people passing by a trail counter within 2 minutes of each other. We compared data from the trail counters with notes from physical observations to ensure accuracy. During this time, Eva Lake had the most hiking traffic per day (mean 21, SE = 2) followed by Abbott Ridge (mean 8, SE = 1) and Avalanche Crest (mean 6, SE = 1).

DOCUMENTING RISK AVOIDANCE

Prey that actively engage in vigilance or other predator monitoring behaviors do so at the cost of other activities such as foraging (Cooper, 2005). To document this potential cost for pikas, we assessed two measures of monitoring behavior: alert distance (D_A) and flight initiation distance (D_F). Alert distance is the distance between a pika and a hiker that causes a pika to stop foraging and become alert to the approaching hiker; it is a measure of risk detection (Taylor and Knight, 2003). Flight initiation distance is a measure of risk tolerance (Ydenberg and Dill, 1986). It describes

the closest distance that an approacher can get before an animal begins to flee (Cooper and Frederick, 2007). We also assessed the ratio of D_F/D_A , how long a pika is willing to postpone flight after becoming alert, as the magnitude of responses could be correlated, but their relative size could vary with pika conditioning to hikers. We estimated the time lost from foraging due to disturbance, which represents an opportunity cost that directly relates to long-term fitness of an animal (Lima, 1998). To capture this cost, we assessed exit delay (T_E) and the delay in return to forage (T_R) after the initial disturbance (Fig. 1). Animals that repeatedly receive nonthreatening disturbance stimuli are expected to postpone flight initiation in favor of monitoring to avoid the opportunity costs and energetic consequences of fleeing (Lima and Dill, 1990; Sirot, 2010). Repeated exposure to nonlethal stimulus has been linked to modified risk assessments and eventual habituation in some species (Taylor and Knight, 2003).

We predicted that human disturbance would negatively affect pikas' foraging activity through pikas' assessment of predation risk and the associated opportunity cost to foraging time (Frid and Dill, 2002). We also predicted that pikas near trails would have a higher tolerance to human disturbance and adapt their behavior to minimize this opportunity cost (Taylor and Knight, 2003).

QUANTIFYING PIKA RESPONSES TO SIMULATED DISTURBANCE BY HIKERS

We simulated hiker disturbance under various conditions and quantified four antipredator behavioral responses for each event (Fig. 1). We conducted disturbance trials from 18 September to 28 September 2012. We confined these to the peak of the haying season to minimize the effects of seasonality on risk behaviors and foraging-predator avoidance trade-offs (Morrison, 2007). The observer sat with binoculars and surveyed patches of talus for occupied pika territories near and away from trails at each site. Following the survey, pikas in each group were randomly selected for disturbance trials. Disturbance trials were conducted on pikas with haypiles ranging from 0 to 490 m away from trails. Individual pikas were sampled only once. Once an active pika was selected for observation, the observer sat with binoculars in the talus >50 m away from the pika territory and waited a minimum of 10 minutes or until the pika no longer visibly responded to the observer's presence and monitored the identified pika until it began foraging. When the target pika was observed foraging for more than 1 minute, one observer (the "hiker") continuously approached at a constant rate of approximately 1 m s⁻¹. Markers were dropped without interrupting the approach (1) at the hiker's starting location, (2) when the pika first became alert to the approaching hiker (D_A), (3) when the pika initiated its flight response (D_F), and (4) at the original position of the pika in the meadow when the trial commenced. The hiker approached the pika either tangentially (at a 90° angle within 2 m of the pika's original location, as if passing by on a trail) or directly. Each treatment was decided at random before the beginning of the trial by consulting a random number table.

The second observer remained at the starting location and recorded the time of behavioral events, with a stopwatch, as soon as the pika became alert to the approaching hiker. After the pika took flight and entered the talus, both observers watched for and signaled when the pika first emerged from cover. The delay in the time it took the pika to emerge from the talus was then recorded (T_E). The observers continued to monitor the pika until the individual resumed foraging in the meadow complex (T_R).

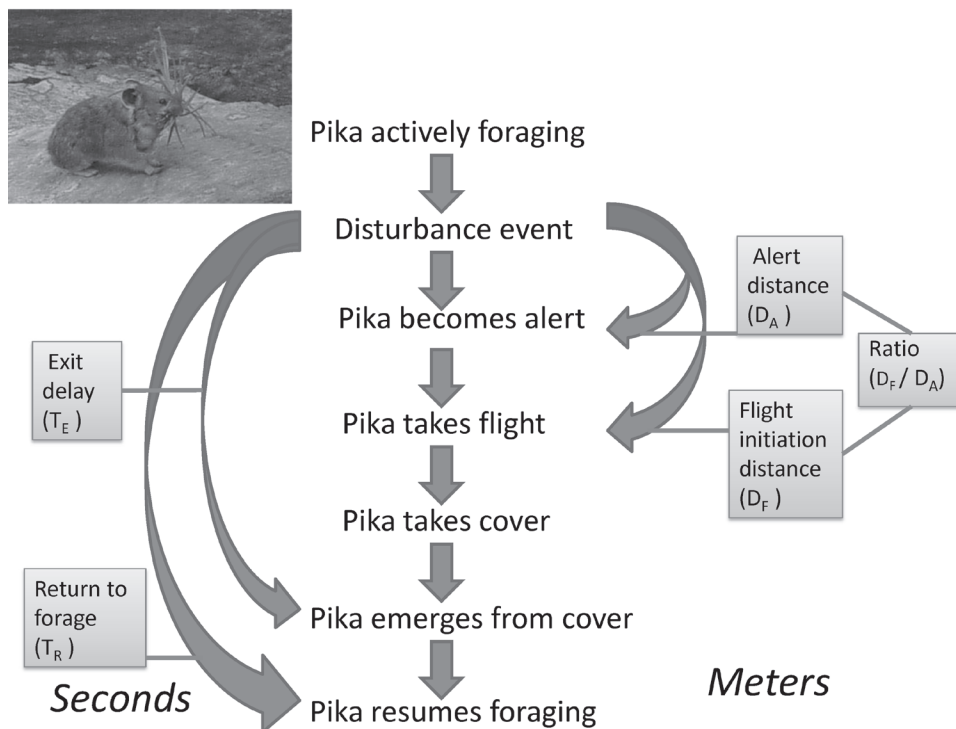


FIGURE 1. Diagram of an American pika's (*Ochotona princeps*) behavioral response to human disturbance. Four antipredator responses: alert distance (D_A), flight initiation distance (D_F), exit delay (T_E), and return to forage (T_R) were measured and recorded for each pika. The ratio between D_F and D_A was assessed to get a measure of pikas' wariness.

Distance to nearest trail was measured using GPS units to the nearest meter from each pika's main haypile. All other measurements were made with a 60-m measuring tape to the nearest tenth of a meter. Of the 48 pikas tested, three did not return to forage due to trials interrupted by hikers not associated with the project. When this occurred the trial was stopped and all other responses were measured and recorded. Temperature was recorded pre-trial as ambient temperature in the shade 0.5 m above ground and ranged from 4.6 °C to 19.3 °C between observations. Temperature change within an observation was minimal as all disturbance trials lasted <30 minutes. All research described in this paper was approved by the University of British Columbia Committee on Animal Care.

QUANTIFYING THE EFFECT OF TEMPERATURE AND EXPOSURE TO HIKERS ON FORAGING TIME

In a separate series of observations, we examined the effect of temperature and distance to trail on pikas' foraging activity, we observed 17 individual pikas for 4–6 hour periods between 21 August to 20 September 2012, for a total of 98 hours of observation time. All foraging activity observations were carried out at the Abbott Ridge field site between 2008 to 2196 m of elevation. These observations were distinct from the hiker disturbance trials because they monitored a single pika throughout a morning,

midday, or evening period and due to the longer observation time (4–6 hours vs. <30 minutes), we were able to observe fewer individuals in this part of the study. Periods of observation were aligned to capture warmer periods during the early afternoon and cooler periods in the morning and evening. Once an active pika was selected for observation, the observers positioned themselves with binoculars in the talus >50 m away from the pika territory and waited a minimum of 10 minutes or until the pika no longer visibly responded to the observer's presence, whichever took longer. For each minute during the observation period the pika's activity was recorded as foraging (eating or haying), vigilance (active monitoring), underground, territorial (marking territory or chasing individuals), traveling, or other. The "other" category ranged from 0% to 1.1% of the total observation time and mainly consisted of grooming. Pika individuals were observed between 8:00 and 18:00 Pacific Time (Table 1). Hiking activity at Abbott Ridge ranged from 4:00 to 21:00 Pacific Time. During the observation period, there was a mean of 7 (SE = 1) groups of hikers per day that passed within a pika's territory for near-trail individuals. There was only one documented hiker passing by observed pikas with haypiles >50 m from an established trail during the observation periods. To ensure consistency between observers, each observer independently recorded the activity of the same pika for 2 hours in a calibration trial. Responses did not vary by more

TABLE 1

Number of hours of pika observation and total number of hiking groups passing by at different times of day from 21 August to 20 September 2012 at Abbott Ridge, Glacier National Park, British Columbia. All times listed are in Pacific Time.

Time of day	8:00	9:00	10:00	11:00	12:00	13:00	14:00	15:00	16:00	17:00
Number of hours of pika observation	9	9	14	14	16	16	8	7	3	3
Total number of hiking groups	4	14	20	26	36	36	41	22	17	1

than 2% between observers. Temperature was recorded every 10 minutes in the shade 0.5 m off the ground and ranged from 4.9 °C to 23.4 °C.

STATISTICAL ANALYSIS

We evaluated support for our predictions using mixed linear models and the information theoretic approach. We used linear mixed effects models (package nlme) to determine the effects of predictors on pikas' antipredator responses (Pineiro et al., 2012). We modeled four responses: D_A , D_F , T_E , and T_R as well as the ratio of D_F to D_A . We modeled each response separately (D_A , D_F , T_E , T_R , and D_F/D_A) and included one factor and four covariates: direction of approach (direct or tangential), distance to trail (m), distance to refuge (m), start distance (m), and temperature (°C). All responses were log transformed to meet assumptions of normality. We included distance to trail rather than hiking traffic in the models as the terms were collinear. Distance to trail more accurately represented the experience of individual pikas that were mid-distance and far from trails where quantifying human traffic using trail counters would have been impractical. When the terms were substituted, they exhibited the same patterns.

Unequal variance in start distance and field site were accounted for with the varIdent function in the nlme package (Pineiro et al., 2012). We included field site as a random effect because we had multiple measurements at each location and there were no significant differences in pikas' antipredator responses between field sites. For each response, we first included all predictors and then analyzed all subsets using the package MuMIn (Barton, 2012). Interaction terms were left out due to small sample size and lack of a priori evidence that suggested their inclusion.

We tested for collinearity between five predictor variables by comparing the variance inflation factor (VIF) values for each covariate using the CAR package (Fox and Monette, 1992). Generally, VIF values greater than 5 are considered to be evidence of collinearity (Fox and Monette, 1992). All the VIF values associated with our five chosen predictors were less than 2.

To estimate the relative effect of distance to trail and temperature on overall foraging behavior we built linear models. We included distance to trail as a proxy for human disturbance events and average ambient temperature in the shade 0.5 m off the ground as predictors of overall foraging activity. An analysis of the hourly data was conducted and found no difference in the strength of the relationship with temperature or other factors, hence the activity data was pooled for each individual over the 4–6 hour observation period to reduce unnecessary complexity and pseudoreplication in the model. Temperatures averaged over each observation period ranged from 7.4 °C to 20.5 °C. There was greater variation in temperature between observation periods (20.2) than within individual periods (2.3). There was no evidence of autocorrelation between time blocks and no significant difference in foraging activity between time periods, so we did not include time as a predictor in the model.

We used the information theoretic approach to compare models and assess their weight of evidence. We started out with a full mixed effects model that included all five predictor variables but no interactions. For all subsequent parsimonious models, second order Akaike Information Criterion (AICc) were computed and models were ranked by lowest AICc with the package MuMIn (Burnham and Anderson, 2002; Barton, 2012). Of all possible subsets, we selected models that fell within $4 \Delta AICc$ ("strong support") of the top model (Burnham and Anderson, 2002). With the established

subset of models, we used model averaging techniques to estimate beta parameters and confidence intervals for all terms included. All analyses were completed in R version 2.15.2 (R Core Development Team, 2012).

Results

All pikas exhibited antipredator responses to human approach and those farther from trails reacted more strongly. Pikas near trails (<50 m) lost on average 4.1 minutes (SE = 0.6, $n = 19$) of foraging time per hiking disturbance while pikas >100 m away from trails lost on average 13.2 minutes (SE = 1.7, $n = 16$) of foraging time per disturbance. Exit delay (T_E), delay in return to forage (T_R), and the ratio of D_F/D_A all decreased with increasing individuals' proximity to trail (Table 2).

Start distance of the hiker relative to the pika had a positive effect on both alert distance (D_A) and flight initiation distance (D_F) (Table 2). Direct approaches were associated with inflated alert distances (D_A) as well as greater delays in return to forage (T_R) (Table 2). Distance to refuge did not influence the direction or magnitude of pikas' antipredator responses in any of the models.

Alert distance ranged from 11.9 to 81.4 m (Table 3) and was affected by direction of approach and start distance, according to the terms in the six best models (Table 2). There was strong support for a negative effect of tangential approach and a positive effect of start distance on D_A as the 95% confidence intervals for neither of the predictors overlapped zero (Fig. 2, part a; Table 2).

All pikas took flight upon approach; their flight initiation distance ranged from 4.7 to 81.4 m (Table 3). Start distance was included in all 11 of the candidate models and had a positive influence on D_F (Fig. 2, part b; Table 2). Direction of approach appeared in six of the 11 candidate models and there was a trend for pikas tangentially approached to have smaller flight initiation distances; however, it and all other predictors in the model had 95% confidence intervals that overlapped zero and were not strongly supported. After they became alert, pikas closer to trails spent more time being vigilant before they took flight than pikas farther from trails (Fig. 2, part e).

Exit delay ranged from 12 to 738 seconds (Table 3). The model with the most support included an intercept term and a predictor for distance to trail, which appeared in 8 of the 11 top models. There was strong support for increasing exit delay with increasing distance to trail (Fig. 2, part c). All other predictors were not supported by the data.

All pikas experienced a disruption in foraging upon human approach. The delay in return to forage after the start of an approach ranged from 53 to 1725 seconds (Table 3). There was strong support for increasing T_R with increasing distance to trail (Fig. 2, part d) and lesser support for decreasing T_R with increasing temperatures. Tangential approach was negatively associated with T_R (Fig. 2, part d). Distance to trail and tangential approach were included in all five candidate models. Temperature was included in three of the top five models. Distance to refuge and initial start distance were less supported by the data and did not have a strong effect on T_R .

FORAGING ACTIVITY

Temperature was strongly supported as a predictor of pikas' foraging activity. Warmer temperatures reduced the proportion of time pikas spent foraging (Fig. 3). Models that included distance to trail received very little support and the term was not included in the top model.

TABLE 2

Model averaged coefficients of four log-transformed anti-predator responses (alert distance [D_A], flight initiation distance [D_F], exit delay [T_E], and delay in return to forage [T_R]) and the ratio of flight initiation distance to alert distance.

Response	Intercept	Start distance (m)	Tangential approach	Distance to trail (m)	Temperature (°C)	Distance to refuge (m)
$\ln(D_A)$	2.421 (SE = 0.135)	0.025 (SE = 0.002)	-0.176 (SE = 0.055)	0.000 (SE = 0.000)	0.013 (SE = 0.008)	-0.033 (SE = 0.032)
$\ln(D_F)$	2.125 (SE = 0.221)	0.023 (SE = 0.004)	-0.260 (SE = 0.132)	0.001 (SE = 0.001)	-0.016 (SE = 0.016)	-0.020 (SE = 0.074)
$\ln(T_E)$	4.314 (SE = 0.499)	-0.003 (SE = 0.008)	-0.229 (SE = 0.290)	0.002 (SE = 0.001)	-0.050 (SE = 0.038)	0.071 (SE = 0.157)
$\ln(T_R)$	6.368 (SE = 0.452)	0.006 (SE = 0.005)	-0.596 (SE = 0.177)	0.003 (SE = 0.001)	-0.050 (SE = 0.024)	0.064 (SE = 0.091)
$\ln(D_F)/\ln(D_A)$	0.733 (SE = 0.135)	-0.001 (SE = 0.002)	-0.076 (SE = 0.072)	0.001 (SE = 0.000)	-0.013 (SE = 0.009)	-0.030 (SE = 0.041)

Note: Coefficients in bold represent variables with CIs that did not overlap zero, thus having a statistically significant effect on the response.

Discussion

Pikas displayed wariness and lost foraging time with each simulated hiking disturbance. Using the predation risk theoretical framework to consider characteristics of the hiker and individual pikas, we were able to determine which variables affected pika's antipredator behaviors in response to human approach.

DID CHARACTERISTICS OF THE HIKER INFLUENCE PIKAS' RESPONSES?

Characteristics of the hiker, specifically directness of approach and start distance, were strong predictors of at least two antipredator responses. This is consistent with the findings of Stankovich and Blumstein (2005), who found that directness of approach is an important predictor of antipredator responses across a wide spectrum of taxa. Predator start distance also influences measures

of wariness among lizards and various species of birds (Blumstein et al., 2003; Cooper, 2005).

The directness with which a predator approaches can be interpreted by the prey as the intent of the predator (Kramer and Bonenfant, 1997). Direct approaches are associated with higher risk in both marmots and black iguanas (Burger and Gochfeld, 1990; Bonenfant and Kramer, 1995). Directness of approach affected pikas' alert distance and return to forage (Table 2). In both cases, tangentially approached pikas showed decreased responses, suggesting that they were perceived as less risky than direct approaches.

A positive effect of start distance on antipredator responses can be attributed to the effort an animal puts into vigilance behavior (Blumstein et al., 2003). Animals in higher risk circumstances are likely to invest more in wariness activities and show inflated responses to increasing start distances (Cooper, 2005). In a number of bird species, the association of flight initiation distance to start distance has been explained as a function of their wariness behav-

TABLE 3

Summary of American pikas' (*Ochotona princeps*) anti-predator responses and predictor variables for hiker disturbance trials. Mean alert distance (D_A), flight initiation distance (D_F), exit delay (T_E), return to forage (T_R), start distance, distance to refuge, distance to trail, and temperature are reported with their standard deviation, range, and associated sample sizes.

Type of approach	Response variables				Predictor variables				
	Alert Distance (D_A) _(m)	Flight Initiation Distance (D_F) _(m)	Exit Delay (T_E) _(sec)	Delay in return to forage (T_R) _(sec)	Start Distance (m)	Distance to refuge (m)	Distance to trail (m)	Temperature (°C)	Sample size
Direct	30.7	22.9	173	764	34.1	1.1	154	12.1	29 ($T_R = 26$)
SD	12.8	12.2	190	486	13	0.6	137	3.6	
Range	14.7–54.3	4.7–52.2	13–738	53–1725	18.0–60.2	0.3–2.7	10–453	5.3–19.3	
Tangential	30.4	20.1	90	354	39.2	1.3	86	13.5	19 ($T_R = 17$)
SD	15.1	15.3	92	219	18.3	0.9	105	3.1	
Range	11.9–81.4	5.5–81.4	12–461	64–977	15.9–91.4	0.2–3.7	0–490	4.6–19.3	
All	30.5	21.2	123	516	37.2	1.2	113	12.9	48 ($T_R = 45$)
SD	14.1	14.1	143	399	16.4	0.8	122	3.3	
Range	11.9–81.4	4.7–81.4	12–738	53–1725	15.9–91.4	0.2–3.7	0–490	4.6–19.3	

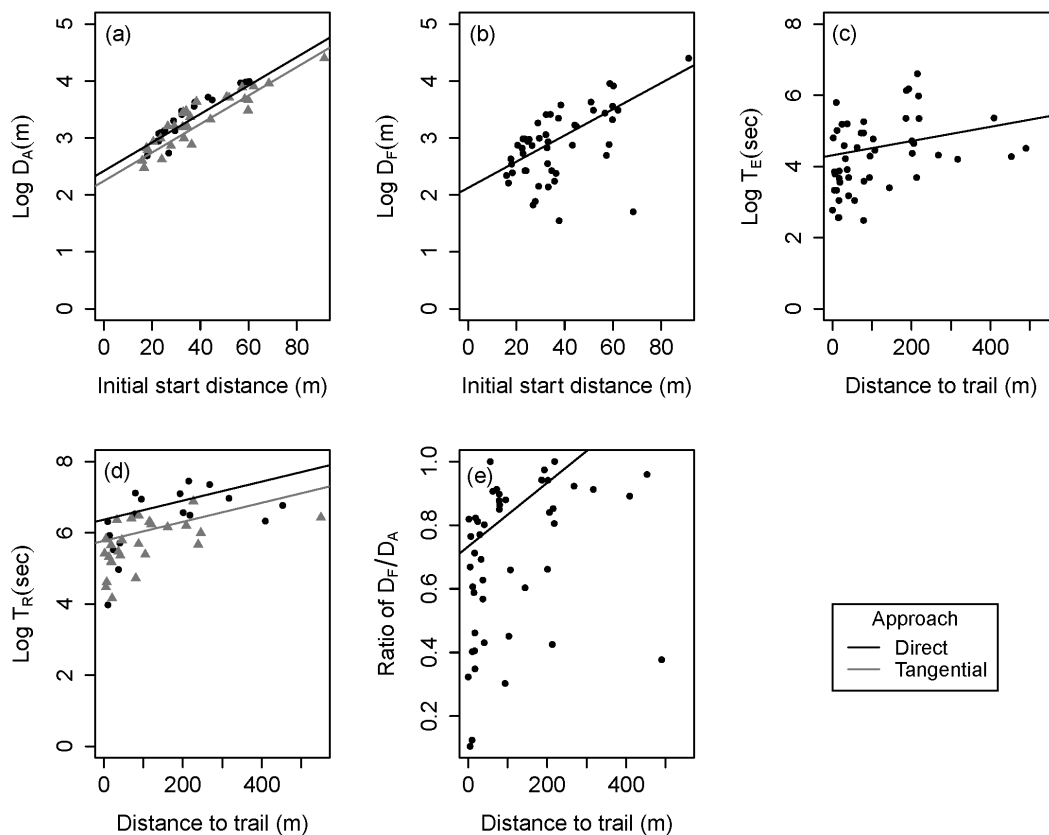


FIGURE 2. (a) American pikas' (*Ochotona princeps*) alert distance, (b) flight initiation distance, (c) exit delay, (d) return to forage, and (e) the ratio of flight initiation distance to alert distance in response to predictors with strong support from the candidate set of models. The slopes and intercepts of the lines drawn are model-averaged estimates from the subset of models within four Δ AICc (Akaike Information Criterion) of the top model; $n = 48$ pikas for (a), (b), (c), and (e) and $n = 45$ for (d). All responses were log transformed to meet the assumptions of the models.

ior (Blumstein et al., 2003). Start distance played an important role in determining pikas' wariness responses (D_F and D_A). Pikas farther from trails took flight sooner after becoming alert, suggesting greater wariness and less tolerance to human approach than pikas regularly exposed to hiking traffic. A similar trend of the influence of start distance on D_F and D_A has been observed in grey squirrels and striped plateau lizards (Cooper, 2005; Engelhardt and Weladji, 2011).

Although not manipulated in these trials, predator group size and speed of approach, both of which vary among hiking groups in the alpine, have been recognized as characteristics that could affect animal flight response (Stankowich and Blumstein, 2005; Cooper and Frederick, 2007).

DID CHARACTERISTICS OF THE INDIVIDUAL PIKA AFFECT RESPONSES?

Experience of the individual affected the magnitude of pikas' responses to disturbance stimuli. Distance to trail, a proxy for individual experience, was strongly supported as a predictor of the opportunity costs of lost foraging time (T_E and T_R) as well as a measure of wariness (D_F/D_A). Decreased responses in pikas nearer to trails could represent an increased, possibly learned, tolerance to human disturbance (Sirot, 2010). Pikas nearer trails may have become accustomed to repeated nonthreatening hiking disturbances and the opportunity cost of fleeing earlier and remaining under cover longer

would not be worth the energy expenditure based on their reassessment of risk (Lima and Dill, 1990). Pikas farther from trails did not have the experience to separate human approach from predator stimulus. Numerous studies with marmots, birds, ungulates, and other taxa have documented deflated responses to human disturbance in animals experiencing repeated nonlethal disturbance stimuli (Burger and Gochfeld, 1990; Griffin et al., 2007; Stankowich, 2008; Sirot, 2010). This reduction in predator avoidance behaviors can lead to habituation (Sirot, 2010). True habituation cannot be established without monitoring individuals over the course of their exposure to human disturbance over time; however, evaluating antipredator behaviors in animals exposed to varying levels of disturbance can increase our understanding of their tolerance to disturbance events (Stankowich and Blumstein, 2005; Bejder et al., 2009; Sirot, 2010).

Distance to refuge was not supported as a strong predictor in any of the responses we recorded. This is contrary to our prediction and numerous studies of pikas and other taxa that suggest that foraging further afield elevates perception of risk (Holmes, 1991; Stankowich and Blumstein, 2005). The relatively low range of distance to refuge (0.2–3.7 m) captured in our study may explain the lack of observed effect. Holmes (1991) found that American pikas would limit their exposure to predation risk by remaining close to cover. He found that female pikas in their second week above ground foraged an average of 4.1 m (SE = 1.3) from the talus; our study did not capture the full upper end of this range.

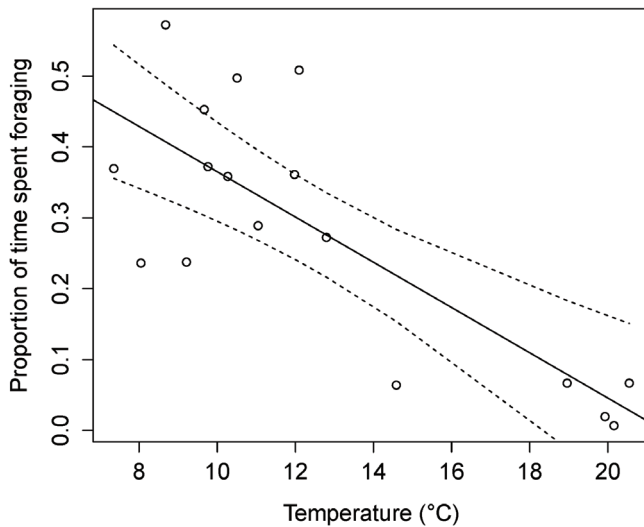


FIGURE 3. The relationship between the proportion of time American pikas (*Ochotona princeps*) spent foraging to average temperature (°C) in the shade 0.5 m off the ground over a 4–6 hour period. Dotted lines represent 95% confidence intervals, $n = 17$ pikas.

Experience of the individual affected the magnitude of pikas' antipredator responses; however, distance to refuge did not. Age, sex, reproductive status, and condition of the animal can all affect the behavioral response to human disturbance (Lima and Dill, 1990; Griffin et al., 2007), and we were not able to control for or measure most of these variables. All animals in our study were adults, ruling out age effects, but we were unable to determine sex and reproductive status without more intrusive capturing and handling methods that may have affected the individual response.

DID TEMPERATURE AFFECT PIKAS' ANTIPREDATOR BEHAVIORS?

Although the range of temperatures captured between disturbance trials was comparable to those between foraging observations, there was not strong support for the influence of environmental temperature on pikas' antipredator responses to human disturbances except in the case of T_R where there was some support of decreasing T_R with increasing temperature. The slight negative relationship between T_R and temperature could be attributed to individual variation where some individuals are more resilient to both environmental and human disturbance. When conducting a meta-analysis on flight initiation distance, Stankowich and Blumstein (2005) reported no consistent response of D_F to temperature across taxa.

PREDICTORS OF PIKAS' FORAGING ACTIVITY

In our pika behavior observation study at Abbott Ridge, temperature was the most important and only significant predictor of pikas' foraging activity over 4–6 hour observation periods. For every degree increase in average daily temperature, pikas decreased foraging by 3% over a 4–6 hour period (Fig. 3). This is consistent with behavioral observations conducted by Smith (1974), who noted that temperature appeared to restrict pikas' foraging activity.

Although human disturbance did affect pikas' antipredator behaviors and reduce foraging time during our simulated hiking study, in the behavioral observation study, distance to trail and therefore general

proximity to hiking traffic did not predict pikas' foraging activity observed over a 4–6 hour period. Pikas near trails exhibited an increased tolerance to human approach (Table 2). This behavioral adaptation could have minimized the influence of human disturbance and helped explain why, over a longer period of several hours, distance to trail was not supported as a predictor of pikas' foraging activity.

BIOLOGICAL RELEVANCE OF HIKING DISTURBANCE

From August to September, pikas near trails at Abbott Ridge encountered an average of 8 (SE = 1) hiking groups per day. We estimated that pikas near trails lost an average of 4.1 (SE = 0.6) minutes of foraging time per hiking disturbance, suggesting that hiking activity results in 33 minutes of total foraging time lost daily. Over this same study period, there was an average of 13.0 (SE = 0.0) hours of daylight (Environment Canada, 2013). Disregarding other factors, human traffic under this scenario would cause a 4% decrease in overall foraging time available to pikas. Compared to the strong negative association of pikas' foraging activity with temperature (Fig. 3), it is not surprising that distance to trail was not a strong predictor for overall pika foraging.

The effect of hiking disturbance at Abbott Ridge may have been minimized by the timing of hiking groups who most often passed by the study site during the early afternoon (Table 1). On hotter days, potential disturbance by hikers in midday hours would be minimized because pikas would be in the talus seeking thermal refuge. Thus, hikers could cause less disturbance if high midday temperatures were already restricting pikas' foraging. The overlap between peak hiking traffic and peak foraging periods will likely vary by location and accessibility as well as time of year.

All foraging activity observations were conducted at the Abbott Ridge site with relatively low amounts of hiking traffic. Had there been greater hiking volumes or more human activity during cooler periods of the day, distance to trail may have had a larger effect on pikas' foraging activity. The maximum number of hiking groups observed in one day at any of the field sites was 48, which could represent a loss of 3.3 hours or 25% of total daylight hours available for foraging. These upper limits of hiking traffic during peak haying periods could meaningfully restrict pika foraging. However, it is not clear what portion of total pika populations in this region are near to hiking trails and thus vulnerable to disturbance. Further study is needed regarding the landscape level footprint and timing of hiking disturbance and pika activity.

IMPLICATIONS FOR CONSERVATION

Although pikas responded to hikers with predator avoidance behaviors in the disturbance trials and there was an opportunity cost to foraging time associated with human disturbance, individuals with prior experience to hikers were able to behaviorally mitigate this impact by adjusting their response. When examining pikas' activity budgets over several hours in a second study, temperature, not distance to trail, was the best predictor of pikas' foraging activity. This suggests that climate warming may reduce time available for pika foraging and food storage, supporting observations of Smith (1974) who proposed that pikas may alter their activity periods to favor cooler temperatures during crepuscular and, potentially, nocturnal periods. Understanding how disturbances affect foraging in the context of daily activity budgets, in addition to acute responses, is important in assessing human impact. Without quantifying activity budgets, we could have reached spurious con-

clusions about the relative importance of temperature and hiking disturbance when it comes to managing a sensitive species.

The interaction between human recreation in the alpine and pikas' thermal limitations needs to be considered when managing populations experiencing these two stressors. When foraging time is limited due to abiotic constraints such as temperature, human disturbance could further hinder the ability of pikas to accumulate adequate food stores. Despite increased tolerance to disturbance by pikas nearer to trails, none of the individuals examined had eliminated their antipredator responses. This suggests that there is a limit to the extent to which animals can habituate to human disturbance stimuli (Frid and Dill, 2002).

To date, eight national parks in the United States are monitoring pika populations for declines. Prior to our study, Parks Canada initiated a pilot Pika Monitoring Project in the Canadian Rockies as part of their mandate to preserve ecological integrity (Timmins and Whittington, 2011). We have shown that hiking traffic and temperature can disrupt foraging by pikas in alpine habitats, and our results suggest that increased climate warming and hiking traffic could have negative effects on pika persistence via reductions in haying. These results may be relevant to management of mountain parks where vulnerable pika populations persist, particularly in warming regions.

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APPENDIX

Table A1

Summary of the time span, range, mean temperatures, and variance corresponding to each pika foraging observation. Times listed are in Pacific Time.

Pika	Observation hours	Temperature (°C)			Variance
		Maximum	Minimum	Mean	
A	8:00–12:00	11.3	6.6	9.2	1.3
B	10:00–16:00	11.4	7.6	9.8	1.0
C	12:00–18:00	13.5	9.1	11.0	1.0
D	8:00–14:00	23.4	13	19.9	9.1
E	10:00–16:00	21.6	18.8	20.5	0.3
F	8:00–14:00	19.1	8.8	14.6	9.3
G	10:00–16:00	22.3	16	19.0	1.7
H	10:00–15:00	21.6	19	20.2	0.6
I	8:00–14:00	11.1	6.1	8.7	2.9
J	8:00–14:00	12.1	4.9	8.0	4.2
K	12:00–18:00	12.8	8.1	9.7	1.9
L	12:00–18:00	11.6	9.4	10.3	0.4
M	8:00–14:00	14.4	10.6	12.0	0.8
N	10:00–16:00	14.1	11.2	12.8	1.0
O	8:00–14:00	12.4	8.8	10.5	1.1
P	8:00–14:00	9.1	5	7.4	1.8
Q	8:00–14:00	14	9.8	12.1	1.5