Quantifying human disturbance on antipredator behavior and flush initiation distance in yellow-bellied marmots

Chunwang Li [a,b], Raquel Monclús [b], Terry L. Maul [c], Zhigang Jiang [a], Daniel T. Blumstein [b,c,*]

[a] Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China
[b] Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095-1606, USA
[c] Rocky Mountain Biological Laboratory, Box 519, Crested Butte, CO 81224, USA

ARTICLE INFO

ABSTRACT

Human disturbance may differentially affect the behavior of wild animals and such behavioral perturbations may have fitness consequences. To understand the effects of specific types of human disturbance on antipredator behavior, a behavior whose performance enhances survival, we studied yellow-bellied marmots (*Marmota flaviventris*). We quantified both antipredator vigilance and the flight initiation distance of the marmots to an approaching human in six different colony sites where we also quantified the frequency and type of human visitation. We developed an analysis framework, using linear mixed models, and found that: (1) when the presence of motorized vehicles and bicycles was high, marmots increased the proportion of time spent vigilant (pseudo $R^2 = 0.33$ and 0.31 for motorized vehicles and bicycles, $P < 0.05$) and decreased the time spent foraging (pseudo $R^2 = 0.29$ and 0.23 for motorized vehicles and bicycles, $P < 0.05$), (2) there was no significant effect of the presence of pedestrians on the time allocated to vigilance and foraging (pseudo $R^2 = 0.25$ and 0.19, $P > 0.05$), (3) marmots decreased the flight initiation distance as disturbance of motorized vehicles (pseudo $R^2 = 0.85$) and pedestrians (pseudo $R^2 = 0.84$) increased ($P < 0.05$), and (4) when we considered bicycles as the disturbance, juveniles tolerated closer approaches than adults or yearlings ($P < 0.001$). Marmots thus responded to some human disturbance by adjusting time spent in foraging and shortening the tolerance distance. Since these behavioral responses could have significant implications for survival and reproduction, we should generally view human disturbance as something that can influence natural antipredator behavior. Importantly, based on an understanding of the differential effects of human activities on wildlife, reducing human disturbance should be taken into account for wildlife management. In addition, our approach will be useful to quantify differential effects of humans on wildlife and to enhance our ability to manage those impacts.

1. Introduction

Animals detect threatening stimuli by allocating time to antipredator vigilance (LaGory, 1987; Treves, 2000), and respond to approaching threats by becoming alert and by fleeing (Fernández-Juricic et al., 2001; Rodgers and Smith, 1997; Ydenberg and Dill, 1986). Because vigilance and other antipredator behaviors have evolved to allow animals to adapt to their environment by minimizing their risk of predation, a fundamental understanding of how humans may influence antipredator behavior is important for developing management plans to allow wildlife to coexist with people.

Humans create a variety of stimuli that may be perceived by non-humans as threatening (Frid and Dill, 2002; Lima and Dill, 1990; Lingle and Wilson, 2001; Steidl and

Anthony, 2000). Moreover, a variety of impacts (e.g., highways, railroads, and trails, and the vehicles, hikers and bikers that use them) may have profound fitness consequences for animals encountering them (Béchet et al., 2003; Burger and Gochfeld, 1991; Ciucci et al., 1997; Elliott et al., 2003; Kerbiriou et al., 2009; Kilgo et al., 1998; Waring et al., 1991).

Road traffic and human activity are known to influence the movements and activity patterns of wild animals, such as elk (*Cervus elaphus* – Creel et al., 2002; Naylor, 2006), mule deer (*Odocoileus hemionus* – Wisdom et al., 2004), Mongolian gazelles (*Procapra gutturosa* – Ito et al., 2005), Przewalski's gazelles (*Procapra przewalskii* – Li et al., 2009), moose (*Alces alces* – Jiang et al., 2007) and alpine marmots (*Marmota marmota* – Neuhaus and Mainini, 1998). Tourists and hiking activities affect behavioral response of alpine marmots (Mainini et al., 1993; Neuhaus and Mainini, 1998) and Olympic marmots (*Marmota olympus* – Griffin et al., 2007).

Despite these previous studies, less is known about whether different human stimuli *differentially* affect antipredator behavior. We focused on yellow-bellied marmots (*Marmota flaviventris*), a widely distributed species in the mountains of Western North America. Yellow-bellied marmots are an excellent model system to understand the consequences of human disturbance because of a rich understanding of their natural antipredator behavior (Blumstein and Armitage, 1997; Blumstein and Daniel, 2004; Blumstein and Munos, 2005; Blumstein et al., 1997, 2004, 2006, 2009), and because they seemingly coexist in a variety of areas with different exposure to humans.

Our study had two main aims. First, we wished to understand how marmot antipredator behavior was influenced by human disturbance. To understand this, we focused on time allocation while foraging and on flight initiation distance. Second, we wished to understand whether various human stimuli differentially affected these antipredator behaviors. To accomplish this, we specifically analyzed different measures of human disturbance and developed a linear mixed modeling methodology that allowed us to identify the importance of different types of human stimuli.

2. Methods

2.1. Study area and animals

Studies were conducted in the Upper East River Valley, in and around The Rocky Mountain Biological Laboratory (RMBL) (38°57′N, 106°59′W), Colorado, USA. The area is extensively used for tourism, but (with very few exceptions) the only human residents are located at the Laboratory itself. For this study, we selected six marmot colonies (including one at the Laboratory) that experienced different degrees of human visitation (Fig. 1). Marmots at all colony sites are routinely trapped and marked with unique ear tags and dyed a unique fur mark by using Nyanzol fur dye (Blumstein et al., 2008). All observations were conducted on individually distinguishable marmots.

2.2. Time allocation

For three summer months (from 20 May to 30 August 2009), and between 7:00 and 16:00 h, we conducted 2-min focal animal observation on foraging marmots (Blumstein et al., 2004). Each marmot was observed three times when it was foraging (they forage intermittently in the morning and late afternoon). Each colony was observed once every 3 days. The behaviors we recorded included foraging (stand foraging and rear foraging), vigilance (stand look and rear look), locomotion (walk and run), other miscellaneous behaviors, and periods of time when animals were out-of-sight behind rocks or vegetation. While observing a marmot, we dictated observations into microcassette recorders and later scored them using JWatcher 1.0 (Blumstein and Daniel, 2007). Before the behavioral observations were undertaken, the observers were trained to identify each behavior with 100% accuracy, and then trained with JWatcher until intra-observer scoring reliability was ≥0.95.

2.3. Quantifying flight initiation distance

We quantified the flight initiation distance (FID), the distance from an approaching threat at which an animal flees (Ydenberg and Dill, 1986) and measured FID of marmots in each colony. FID measures were taken independently to focal foraging observation. To minimize habituation to frequent disturbance, repeated observations had an interval of >5 days. Each marmot was approached and FID was measured at least three times, each on a different day. We approached subjects at 0.5 m/s (observers were trained to 95% accuracy before starting data collection), and dropped flags to note when they fled. We then used a laser rangefinder (Yardagepro 400, Bushnell Performance Optics, USA) to measure key distances that included start distance (the distance from the observer to the subject when the observer started walking towards it), flight initiation distance, and distance to burrow (the distance between the subject and the burrow when it initially moved). We used a clinometer to measure the incline where the marmot was when we initiated the approach. We categorized the incline as 0–10°, 10–30° and >30°. Before doing our approach experiment, all observers were trained to walk consistently at 0.5 m/s.

2.4. Human disturbance data

At the peak of the tourist season (late June to mid July), we quantified human disturbance, every other day, for a total of 12 days. From 7:00 to 18:00 h, we continuously recorded the presence of motorized vehicles, bicycles and persons that stayed or passed through or within 300 m of each colony and calculated the frequency of occurrence. Human disturbances were recorded independently of the behavioral observations and collection of FID data.

From these observations, we calculated a pedestrians, bicycles, and total vehicles disturbance index for each colony. The index was calculated correcting the frequency of occurrence of each disturbance for the distance from the disturbance to the edge of the colony. The index cal-
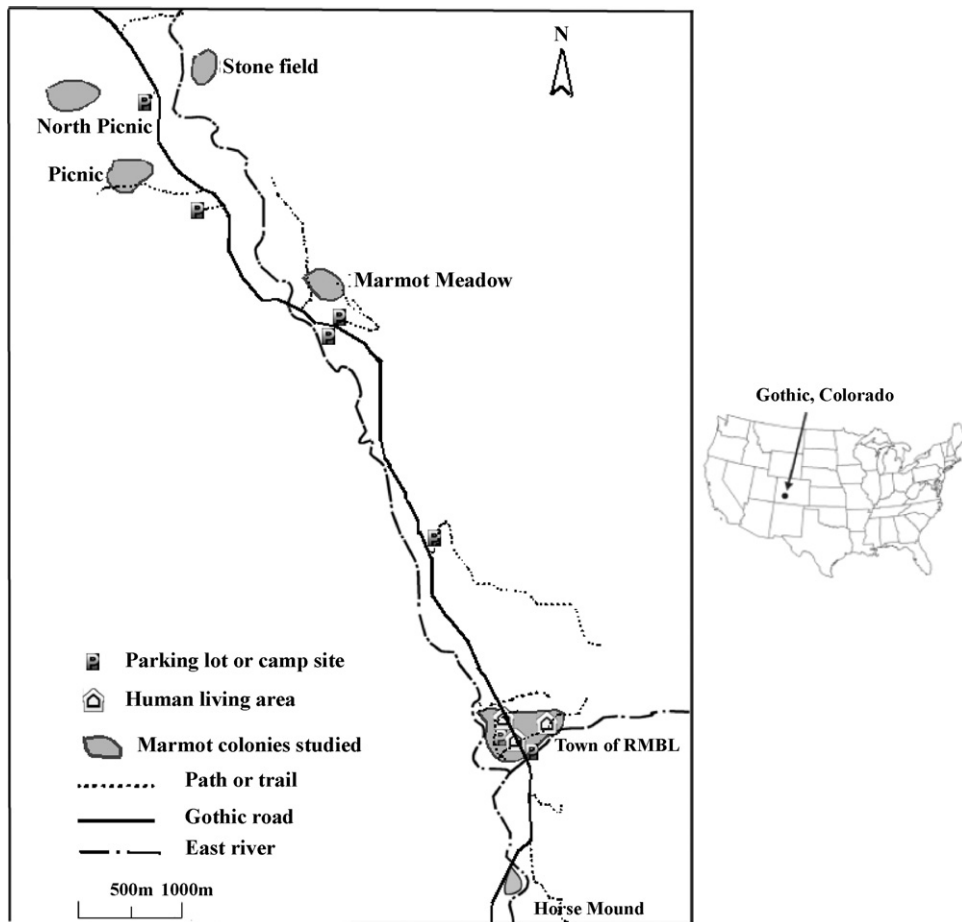
Fig. 1. Residential area, Gothic road, and marmot colonies studied in relation to the Rocky Mountain Biological Laboratory, Gothic, Colorado, USA.

culated for pedestrians followed a bimodal distribution, so we categorized the colonies as having low or high pedestrian pressure. Moreover, considering the distribution of the total vehicular index, each colony was categorized as having low, medium or high vehicular pressure.

2.5. Statistical analysis

We fitted linear mixed models, calculated with the function lmer from the package lme4 from the software package R version 2.10.1 (R Development Core Team, 2009). We ensured that the residuals of all models approximated to a normal distribution by visually checking normal probability plots and by the Shapiro–Wilk test. The proportion of time vigilant and foraging were arcsine transformed, whereas FID was $[x^{0.2}]$ transformed prior to analysis.

To test for the effect of human disturbance on the proportion of time allocated to different activities we included in the model, as fixed factors, the marmot's age and sex, and the index of human disturbance (total vehicles and pedestrians as categorical variables and bicycles as a continuous variable, one at a time). We included the interaction between the index of human disturbance and age, and when not significant, removed the interaction from the final model (Engqvist, 2005). For the analysis of flight

initiation distance we also included as explanatory variables the observer's starting distance, the incline of the land where the marmot was when we initiated the approach, and the distance the marmot was to its nearest burrow. In all cases (time allocation and flight initiation distance) the identity of the focal animal was included as a random factor to control for repeated measures. Moreover, the colony they came from was also included as a random factor. The significance of model parameters was estimated by comparisons to a probability distribution obtained by 10,000 Markov Chain Monte Carlo simulations with the function pvals.fnc from package language R (for further details see Baayen et al., 2008). The global models were compared using Nagelkerke's pseudo R^2 (Nagelkerke, 1991).

3. Results

3.1. Time allocation

We collected data from a total of 96 individuals on 309 occasions (50 females: 23 adults, nine yearlings and 18 juveniles; 46 males: 11 adults, 14 yearlings and 21 juveniles). We found differences in the time allocated to different activities (vigilance and foraging) in relation to our measures of human disturbance pressure (see Table 1).

Table 1
Mixed-effects model testing for the effect of human disturbance on the proportion of time marmots allocated to vigilance and foraging.

	Proportion of time vigilant					Proportion of time foraging				
	$\overline{\theta}$	HPD95 lower	HPD95 upper	P_{MCMC}	Pseudo R^2	$\overline{\theta}$	HPD95 lower	HPD95 upper	P_{MCMC}	Pseudo R^2
(a) Total vehicles					0.33					0.29
(Intercept)	0.509	0.415	0.605	<0.001		0.944	0.82	1.066	<0.001	
Total vehicles$_{medium}$	0.052	−0.060	0.169	0.305		−0.047	−0.207	0.108	0.439	
Total vehicles$_{high}$	0.215	0.094	0.334	0.007		−0.264	−0.444	−0.112	0.01	
Age$_{juvenile}$	−0.181	−0.235	−0.122	<0.001		0.160	0.107	0.218	<0.001	
Age$_{yearling}$	−0.025	−0.091	0.037	0.437		0.034	−0.028	0.098	0.29	
Sex$_{male}$	0.027	−0.019	0.074	0.253		0.007	−0.039	0.055	0.764	
(b) Bicycles					0.31					0.23
(Intercept)	0.394	0.272	0.515	<0.001		1.079	0.842	1.335	<0.001	
Bicycles	0.203	0.094	0.316	<0.001		−0.248	−0.494	−0.038	0.032	
Age$_{juvenile}$	−0.185	−0.241	−0.128	<0.001		0.157	0.105	0.215	<0.001	
Age$_{yearling}$	−0.028	−0.092	0.032	0.371		0.039	−0.020	0.102	0.201	
Sex$_{male}$	0.032	−0.016	0.079	0.188		0.006	−0.040	0.054	0.789	
(c) Pedestrians					0.25					0.19
(Intercept)	0.716	0.512	0.929	<0.001		0.723	0.445	1.024	0.001	
Pedestrians$_{low}$	−0.144	−0.374	0.086	0.152		0.136	−0.203	0.433	0.328	
Age$_{juvenile}$	−0.177	−0.235	−0.120	<0.001		0.152	0.095	0.207	<0.001	
Age$_{yearling}$	−0.025	−0.091	0.040	0.445		0.039	−0.029	0.098	0.235	
Sex$_{male}$	0.029	−0.018	0.077	0.225		0.007	−0.039	0.054	0.758	

Note: Human disturbance was measured as (a) total vehicles (high, medium, low), (b) bicycles per hour and (c) pedestrians (high, low). The table shows the mean estimate ($\overline{\theta}$), the Bayesian highest posterior density confidence interval (HPD 95 lower, HPD 95 upper), the P values (P_{MCMC}), and Nagelkerke's pseudo R^2.

Results from our post hoc analyses suggest that marmots increased the proportion of time vigilant when the presence of vehicles was high (low vs. high P_{MCMC} = 0.032; medium vs. high P_{MCMC} = 0.038), though we found no differences between the proportion of time spent vigilant under low and medium vehicular pressure (P_{MCMC} = 0.514) (Fig. 2). We found similar results when we considered the effect of bicycles (Table 1). While marmots increased the time spent vigilant due to motorized vehicles and bicycles, they decreased the time spent foraging (Table 1 and Fig. 2). The effect was apparent when the proportion of vehicles and bicycles was high (for total vehicles: low vs. high P_{MCMC} = 0.026; medium vs. high = 0.030; low vs. medium = 0.628). We found no effect of the presence of pedestrians on the time allocated to different activities (Table 1). In the three models we found that juveniles spent significantly less time vigilant than yearlings and adults (juveniles vs. yearlings P_{MCMC} = 0.001; juveniles vs. adults P_{MCMC} = 0.001). However, yearlings and adults did not differ in the time allocated to vigilance or foraging (P_{MCMC} = 0.268). The model containing the variable Total Vehicles explained 33% of the variation of the proportion of time vigilant and 29% of the time spent foraging (pseudo R^2 = 0.33 and 0.29, respectively), whereas the model that explained less variation was the one that included the variable Pedestrians (pseudo R^2 = 0.25 and 0.19). We found no sex effects on the time allocated to vigilance or foraging (Table 1), and none of the interactions between human disturbance and age were significant (all P_{MCMC} > 0.1), and were removed from the final models.

3.2. Flight initiation distance

We made 176 approaches to 92 identified marmots from six different colonies (45 females, of which 17 were adults, nine yearlings and 19 juveniles; 47 males, of which 13 were adults, 13 yearlings and 21 juveniles). Marmots tolerated closer approaches as any type of human disturbance increased (Table 2 and Fig. 3) and these models explained similar amounts of variation in FID (pseudo R^2 = 0.85; 0.83; 0.84 for total vehicles, bicycles and pedestrians, respectively). However, given a constant amount of disturbance, marmots showed a stronger response to pedestrians than to any other type of disturbance (Fig. 3). In addition, when we focused on the effect of bicycles, we found that juveniles had shorter FID than adults and yearlings (Table 2). When the human disturbance variables were bicycles and pedestrians we found a positive and significant relationship between the distance to the burrow and the FID: the further away from their burrow, the earlier the marmots reacted to the approach (when bicycle, P_{MCMC} = 0.036; when pedestrians, P_{MCMC} = 0.015).

4. Discussion

Marmot time allocation was affected by high human disturbance: marmots increased their proportion of time spent vigilant and decreased the time spent foraging with increased motorized vehicle and bicycle traffic. Indeed, previous studies found that a variety of animals adapt to human activities by changing vigilance behavior (Burger and Gochfeld, 1990; Fernández-Juricic and Schroeder, 2003; Papouchis et al., 2001; Wang et al., 2004). For any given level of disturbance, and any given starting distance, flight initiation distance was differentially influenced by the type of disturbance; marmots were most responsive to pedestrians, and least responsive to bicycles (Fig. 3). Additionally, marmots tolerated closer experimental approaches as the disturbance from motorized vehicles and pedestrians increased. Previous studies have also found

Table 2
Mixed-effects model testing for the effect of human disturbance on marmot flight initiation distance.

	Flight initiation distance				
	$\bar{\theta}$	HPD95 lower	HPD95 upper	P_{MCMC}	Nagelkerke's pseudo R^2
(a) Total vehicles					0.85
Total vehicles$_{\text{low}}$	7.175	4.511	9.746	<0.001	
Total vehicles$_{\text{medium}}$	5.133	3.71	6.613	<0.001	
Total vehicles$_{\text{high}}$	2.088	1.297	3.058	<0.001	
Start distance	0.061	0.049	0.073	<0.001	
Total vehicles$_{\text{low}}$ × start distance	−0.043	−0.06	0.026	<0.001	
Total vehicles$_{\text{medium}}$ × start distance	−0.052	−0.068	−0.037	<0.001	
Age$_{\text{yearling}}$	−0.251	−0.919	0.380	0.441	
Age$_{\text{adult}}$	0.011	−0.495	0.513	0.964	
Sex$_{\text{male}}$	−0.169	−0.592	0.220	0.415	
Incline	−0.029	−0.552	0.490	0.908	
Distance to burrow	0.018	−0.009	0.041	0.165	
(b) Bicycles					0.83
Bicycles	−4.794	−7.539	−1.985	0.001	
Start distance	−0.008	−0.023	0.009	0.349	
Bicycles × start distance	0.038	0.022	0.052	0.036	
Age$_{\text{juvenile}}$	9.336	5.821	12.697	<0.001	
Age$_{\text{yearling}}$	9.151	5.686	12.572	<0.001	
Age$_{\text{adult}}$	9.332	5.884	12.730	<0.001	
Sex$_{\text{male}}$	−0.272	−0.694	0.144	0.204	
Incline	−0.090	−0.630	0.439	0.747	
Distance to burrow	0.029	0.003	0.052	0.036	
(c) Pedestrians					0.84
Pedestrians$_{\text{low}}$	5.079	3.825	6.367	<0.001	
Pedestrians$_{\text{high}}$	1.618	−0.265	3.45	0.081	
Start distance	0.072	0.059	0.086	<0.001	
Pedestrians$_{\text{low}}$ × start distance	−0.053	−0.068	−0.038	<0.001	
Age$_{\text{yearling}}$	−0.027	−0.630	0.574	0.934	
Age$_{\text{adult}}$	−1.395	−0.627	0.345	0.575	
Sex$_{\text{male}}$	−0.149	−0.538	0.265	0.451	
Incline	0.012	−0.481	0.501	0.964	
Distance to burrow	0.028	0.006	0.051	0.015	

Note: Human disturbance was measured as (a) total vehicles (high, medium, low), (b) bicycles per hour and (c) pedestrians (high, low). The table shows the mean estimate ($\bar{\theta}$), the Bayesian highest posterior density confidence interval (HPD 95 lower, HPD 95 upper), the *P* values (P_{MCMC}), and the Nagelkerke's pseudo R^2.

that alert distance decreased as a result of repeated exposure to humans (Lord et al., 2001; Miller et al., 2001; Smit and Visser, 1993). Neuhaus and Mainini (1998) also found that alpine marmots in frequently disturbed areas showed less reaction to hiking activities than marmots in more remote areas.

The impact of human activities on marmots was age-dependent. Juveniles spent significantly less time vigilant than yearlings and adults. We also found age-specific effects of bicycle disturbance on FID: juveniles tolerated closer approaches than adults and yearlings. Borrego et al. (2008) revealed that, in yellow-bellied marmots, the survival of juveniles varied over time and among sites, whereas that of yearlings varied among sites but not over time. The survival of adults did not vary significantly over time or among sites. Moreover, the risk of being killed by a badger was highest for young marmots, intermediate for yearlings, and lowest for adults (Armitage, 2004). It is conceivable that age differences of spatiotemporal variation in survival of yellow-bellied marmots could relate to age-specific antipredator behavior. Together with the similar study in alpine marmots (Neuhaus and Mainini, 1998), we suggest that an assessment of risk is built up gradually during growth and development.

There are at least two reasons to explain why marmots in areas with different disturbance intensities show different patterns of time allocation as well as different flight behavior. First, they modify time allocation because they need to assess their total risk and acquire information of what is happening around them. Thus, they increase vigilance. Second, they have learnt either that humans are not a huge threat or that humans move slowly so they tolerate closer approaches. Together, marmots may spend more time being vigilant but they tolerate closer approaches. Importantly, change in time allocation may have fitness consequences (e.g., Bouskila, 1995; Brown, 1999). If we had only looked at flight initiation distance, we would have been led to a spurious conclusion about the potential effects of humans on marmots.

Our data indicated that yellow-bellied marmots still live in highly disturbed areas, such as RMBL, despite disturbance. Louzã (2007) suggested that a few wild animal species adapt themselves to human activity and become synanthropic while maintaining their natural behavior. In support of this, marmots are commonly (but certainly not exclusively) found around people in other areas in their range. One possible benefit from associating with humans is a decreased risk of predation if the presence of humans reduces the presence of some of their preda-
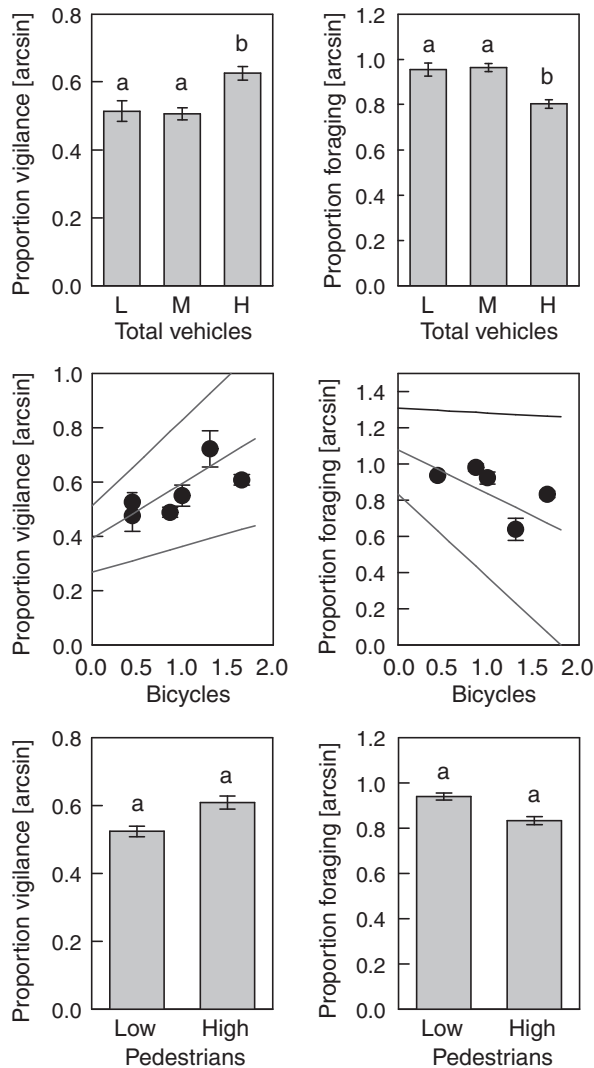
Fig. 2. The effect of the presence of (upper) motorized vehicles, (middle) bicycles and (lower) pedestrians on the proportion of time that the marmots spent vigilant (1) and foraging (2) (mean ± SE). The graphs represent the transformed data, and in the case of the presence of bicycles, the thicker line represents the predicted values, whereas the thinner lines represent the predicted upper and lower limits. For motorized vehicles (upper) and pedestrians (lower) the different letters indicate significant differences, see text for statistics.

tors. Blumstein and Armitage (1997) reported that there are eight predators that killed yellow-bellied marmots in our study area. Among those predators, coyote (*Canis latrans*), badger (*Taxidea taxus*) and black bear (*Ursus americanus*) were considered to be the main threats (see Blumstein and Armitage, 1997; van Vuren, 1991, 2001). Based on our observations, these predators were most commonly sighted in areas with low human disturbance, whereas in the areas with high human disturbance we only saw red fox (*Vulpes vulpes*) and long-tailed weasels (*Mustela frenata*) during our study. We have no precise data on predation rates in the different areas, but previous studies showed that frequent human activities cause predators to live far from human activity and to increase nocturnal activity and
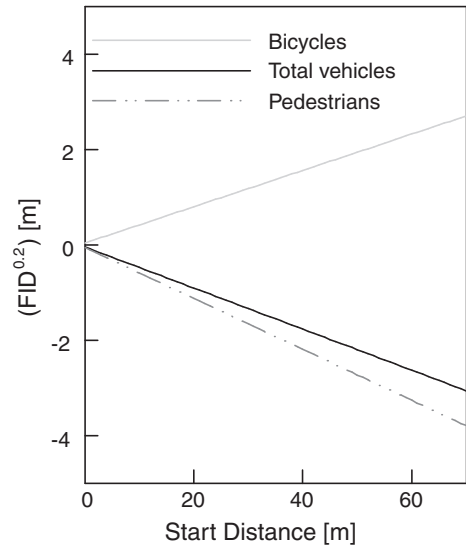

Fig. 3. Relationships between marmot flight initiation distance (FID) and the starting distance, at a given human disturbance pressure (=1), to total vehicles (grey line), bicycles (black line) and pedestrians (grey dotted line). The lines represent the predicted values. Note that data are transformed to meet assumptions of our models.

decrease diurnal activity (e.g., in coyotes, see McClennen et al., 2001; Riley et al., 2003). Thus, for marmots, high disturbance areas may scare away key predators and make those areas predator-free and hence, safer. Our observations indicated that marmots increased their vigilance behavior when human disturbance in some areas increased, however they could have benefited from reduced predation risk in areas with higher disturbance.

5. Conclusion

Our findings suggested that long-term, high-level, human disturbance affected yellow-bellied marmot antipredator behavior. More generally, our study shows that it is important to study the effects of different stimuli because animals may respond differently to them; realize that there may be age-dependent effects; and study different antipredator behaviors to obtain a comprehensive understanding of the effects of humans on predation risk management. Future studies may adopt both our mix of experimental and observational studies combined with mixed effects models to identify and isolate differential effects of humans on wildlife. Doing so should enhance our ability to manage those impacts.

References

Armitage, K.B., 2004. Badger predation on yellow-bellied marmots. Am. Midl. Nat. 151, 378–387.

Baayen, R.H., Davidson, D.J., Bates, D.M., 2008. Mixed-effects modeling with crossed random effects for subjects and items. J. Mem. Lang. 59, 390–412.

Béchet, A., Giroux, J.F., Gauthier, G., Nichols, J.D., Hines, J.E., 2003. Spring hunting changes the regional movements of migrating greater snow geese. J. Appl. Ecol. 40, 553–564.

Blumstein, D.T., Armitage, K.B., 1997. Alarm calling in yellow-bellied marmots. I. The meaning of situationally variable alarm calls. Anim. Behav. 53, 143–171.

Blumstein, D.T., Daniel, J.C., 2004. Yellow-bellied marmots discriminate between the alarm calls of individuals and are more responsive to the calls from pups. Anim. Behav. 68, 1257–1265.

Blumstein, D.T., Daniel, J.C., 2007. Quantifying Behavior The JWatcher Way. Sinauer, Sunderland, MA.

Blumstein, D.T., Munos, O., 2005. Individual and age/sex class variation in marmot alarm calls. Anim. Behav. 69, 353–361.

Blumstein, D.T., Cooley, L., Winternitz, J., Daniel, J.C., 2008. Do yellow-bellied marmots respond to predator vocalizations? Behav. Ecol. Sociobiol. 62, 457–468.

Blumstein, D.T., Ferando, E., Stankowich, T., 2009. A test of the multipredator hypothesis: yellow-bellied marmots respond fearfully to the sight of novel and extinct predators. Anim. Behav. 78, 873–878.

Blumstein, D.T., Ozgul, A., Yovovitch, V., Van Vuren, D.H., Armitage, K.B., 2006. Effect of predation risk on the presence and persistence of yellow-bellied marmot (*Marmota flaviventris*) colonies. J. Zool. 270, 132–138.

Blumstein, D.T., Steinmetz, J., Armitage, K.B., Daniel, J.C., 1997. Alarm calling in yellow-bellied marmots. II. The importance of direct fitness. Anim. Behav. 53, 173–184.

Blumstein, D.T., Runyan, A., Seymour, M., Nicodemus, A., Ozgul, A., Ransler, F., Im, S., Stark, T., Zugmeyer, C., Daniel, J.C., 2004. Locomotor ability and wariness in yellow-bellied marmots. Ethology 110, 615–634.

Bouskila, A., 1995. Interactions between predation risk and competition: a field study of kangaroo rats and snakes. Ecology 76, 165–178.

Borrego, N., Ozgul, A., Armitage, K.B., Blumstein, D.T., Oli, M.K., 2008. Spatiotemporal variation in survival of male yellow-bellied marmots. J. Mammal. 89, 365–373.

Brown, J.S., 1999. Vigilance, patch use and habitat selection: foraging under predation risk. Evol. Ecol. Res. 1, 49–71.

Burger, J., Gochfeld, M., 1990. Risk discrimination of direct versus tangential approach by basking black iguanas (*Ctenosaura similis*): variation as a function of human exposure. J. Comp. Psychol. 104, 388–394.

Burger, J., Gochfeld, M., 1991. Human activity influence and diurnal and nocturnal foraging of sanderlings (*Calidris alba*). Condor 93, 259–265.

Ciucci, P., Boitani, L., Francisci, F., Andreoli, G., 1997. Home range, activity and movements of a wolf pack in central Italy. J. Zool. 243, 803–819.

Creel, S., Fox, J.E., Hardy, A., Sands, J., Garrott, B., Peterson, R.O., 2002. Snowmobile activity and glucocorticoid stress responses in wolves and elk. Conserv. Biol. 16, 809–814.

Elliott, C., Swarthout, H., Steidl, R.J., 2003. Experimental effects of hiking on breeding Mexican spotted owls. Conserv. Biol. 17, 307–315.

Engqvist, L., 2005. The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. Anim. Behav. 70, 967–971.

Fernández-Juricic, E., Schroeder, N., 2003. Do variations in scanning behavior affect tolerance to human disturbance? Appl. Anim. Behav. Sci. 84, 219–234.

Fernández-Juricic, E., Jimenez, M.D., Lucas, E., 2001. Alert distance as an alternative measure of bird tolerance to human disturbance: implications for park design. Environ. Conserv. 28, 263–269.

Frid, A., Dill, L.M., 2002. Human-caused disturbance stimuli as a form of predation risk. Conserv. Ecol. 6 (1), 11.

Griffin, S.C., Valois, T., Mark, L., Taper, M.L., Mills, L.S., 2007. Effects of tourists on behavior and demography of Olympic marmots. Conserv. Biol. 21 (4), 1070–1081.

Ito, T.Y., Miura, N., Lhagvasuren, B., Enkhbileg, D., Takatsuki, S., Tsunekawa, A., Jiang, Z., 2005. Preliminary evidence of a barrier effect of a railroad on the migration of Mongolian gazelles. Conserv. Biol. 19, 945–948.

Jiang, G., Zhang, M., Ma, J., 2007. Effects of human disturbance on movement, foraging and bed site selection of red deer *Cervus elaphus xanthopygus* in the Wandashan mountains, northeastern China. Acta Theriol. 52, 435–446.

Kerbiriou, C., Le Viol, L., Robert, A., Porcher, E., Gourmelon, F., Julliard, R., 2009. Tourism in protected areas can threaten wild populations: from individual response to population viability of the chough *Pyrrhocorax pyrrhocorax*. J. Appl. Ecol. 46, 657–665.

Kilgo, J.C., Labisky, R.F., Fritzen, D., 1998. Influences of hunting on the behavior of white-tailed deer: implications for conservation of the Florida panther. Conserv. Biol. 12, 1359–1364.

LaGory, K.E., 1987. The influence of habitat and group characteristics on the alarm and flight response of white-tailed deer. Anim. Behav. 35, 20–25.

Li, C., Jiang, Z., Feng, Z., Yang, X., Yang, J., Chen, L., 2009. Activity pattern of Przewalski's gazelle is affected by a new highway. Wildl. Res. 36, 379–385.

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640.

Lingle, S., Wilson, W.F., 2001. Detection and avoidance of predators in white-tailed deer *Odocoileus virginianus* and mule deer *O. hemionus*. Ethology 107, 125–147.

Lord, A., Waas, J.R., Innes, J., Whittingham, M.J., 2001. Effects of human approaches to nests of northern New Zealand dotterel. Biol. Conserv. 98, 233–240.

Louzã, A.C., 2007. The sharing of urban areas by man and animals: pleasure and risk. In: Pereira, M.S. (Ed.), A Portrait of State-of-the-Art Research. Technical University of Lisbon, Springer, Berlin, Germany, pp. 479–488.

Mainini, B., Neuhaus, P., Ingold, P., 1993. Behaviour of marmots marmota marmota under the influence of different hiking activities. Biol. Conserv. 64 (2), 161–164.

McClennen, N., Wigglesworth, R.R., Anderson, S.H., Wachob, D.G., 2001. The effect of suburban and agricultural development on the activity patterns of coyotes (*Canis latrans*). Am. Midl. Nat. 146 (1), 27–36.

Miller, S.G., Knight, R.L., Miller, C.K., 2001. Wildlife responses to pedestrians and dogs. Wildl. Soc. Bull. 29, 124–132.

Nagelkerke, N.J.D., 1991. A note on a general definition of the coefficient of determination. Biometrika 78, 691–692.

Naylor, L.M., 2006. Behavioral Responses of Rocky Mountain Elk (*Cervus elaphus*) to Recreational Disturbance. Master Thesis, Oregon State University, Oregon, USA.

Neuhaus, P., Mainini, B., 1998. Reactions and adjustment of adult and young alpine marmots *Marmota marmota* to intense hiking activities. Wildl. Biol. 4, 119–123.

Papouchis, C., Singer, F.J., Sloan, W.B., 2001. Responses of desert bighorn sheep to increased human recreation. J. Wildl. Manage. 65, 573–582.

R Development Core Team, 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, http://www.R-project.org.

Riley, S.P.D., Sauvajot, R.M., Fuller, T.K., York, E.C., Kamradt, D.A., Bromley, C., Wayne, R.K., 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. Conserv. Biol. 17 (2), 566–576.

Rodgers, J.A., Smith, H.T., 1997. Buffer zone distances to protect foraging and loafing waterbirds from human disturbance in Florida. Wildl. Soc. Bull. 25, 139–145.

Smit, C.J., Visser, G.J.M., 1993. Effects of disturbance on shorebirds: a summary of existing knowledge from the Dutch Wadden Sea and Delta area. Wader Study Group Bull. 68, 6–19.

Steidl, R.J., Anthony, R.G., 2000. Experimental effects of human activity on breeding bald eagles. Ecol. Appl. 10, 258–268.

Treves, A., 2000. Theory and method in studies of vigilance and aggregation. Anim. Behav. 60, 711–722.

van Vuren, D., 1991. Yellow-bellied marmots as prey of coyotes. Am. Midl. Nat. 125, 135–139.

van Vuren, D.H., 2001. Predation on yellow-bellied marmots (*Marmota flaviventris*). Am. Midl. Nat. 145, 94–100.

Wang, Y., Chen, S., Ding, P., 2004. Flush distance: bird tolerance to human intrusion in Hangzhou. Zool. Res. 25, 214–220.

Waring, G.H., Griffis, J.L., Vaughn, M.E., 1991. White-tailed deer roadside behavior, wildlife warning reflectors, and highway mortality. Appl. Anim. Behav. Sci. 29, 215–223.

Wisdom, M.J., Preisler, H.K., Cimon, N.J., Johnson, B.K., 2004. Effects of off-road recreation on mule deer and elk. In: Rahrn, J. (Ed.), Transactions of the 69th North American Wildlife and Natural Resources Conference. Wildlife Management Institute, Washington, DC, USA, pp. 531–550.

Ydenberg, R.C., Dill, L.M., 1986. The economics of fleeing from predators. Adv. Study Behav. 16, 229–249.