



Original Article

Habituation or sensitization? Long-term responses of yellow-bellied marmots to human disturbance

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Continuous exposure to humans causes wildlife to either habituate or sensitize. Although increased tolerance may play an important role in coexistence with humans, the mechanisms and fitness outcomes of long-term changes of tolerance are not fully understood because only a few studies have assessed individual- and population-level responses over many years. We developed a novel predictive framework to study habituation and sensitization to humans and applied it to yellow-bellied marmots (*Marmota flaviventer*) in areas of high and low human disturbance. We focused on two antipredator behaviors—time allocation to vigilance during foraging to quantify baseline vigilance levels and flight initiation distance (FID)—to quantify subsequent responsiveness to threat. We used the rate of body mass gain during the active season as a fitness outcome. Assessing 15 years' population and individual-level responses to human disturbances, marmots in highly disturbed colonies allocated more time to vigilance, but this did not change over time. FID decreased on average when they were approached more and also tended to decrease in highly disturbed colonies and over 15 years. Yet, there was individuality in FIDs; marmots that fled at greater distances became sensitized with repeated approaches. Additionally, the marmots in highly disturbed colonies gained less body mass over time compared to conspecifics in less disturbed colonies. These results suggested that, although marmots habituated to humans, long-term human disturbance has negative fitness consequences. Our framework should help wildlife managers evaluate the comprehensive impact of human activities on wildlife.

Key words: antipredator behavior, ecotourism, flight initiation distance, habituation, human impact, vigilance

INTRODUCTION

The increase in urban areas and the popularity of outdoor activities has resulted in wildlife increasingly exposed to humans, which has reduced biodiversity. For many animals, humans are a “super predator” (Darimont et al. 2015), and human-caused mortality is one of the main drivers of species extinction (Darimont et al. 2015). Indeed, human activities have killed far more animals than genuine predators. To minimize the effects of anthropogenic activities, animals modify a variety of behaviors (Lowry et al. 2013; Fleming and Bateman 2018). Sensitization to humans (the behavioral process that leads to increased responsiveness toward particular threats; Blumstein 2013) is a key behavioral modification to avoid humans. For example, long-term hunting activity has increased wild reindeer *Rangifer tarandus* flight initiation distance (FID: the distance at which animals flee from approaching

humans; Ydenberg and Dill 1986; Cooper and Blumstein 2015) in southern Norway over 14 years (Reimers et al. 2009), indicating that continuous human disturbance has sensitized reindeers to humans. While it would be adaptive to be sensitized if humans create threats to animals, such increased responsiveness may reduce the time and energy available for fitness-enhancing activities, such as foraging and reproduction. Therefore, sensitization may decrease individual fitness and population growth through reduced body mass (Harris and Carr 2016) and reproductive success (Zanette et al. 2011). However, animals may also habituate to humans (the behavioral process that leads to reduced responsiveness to humans with repeated exposure). Many studies have shown that animals in urban areas decrease their responsiveness to humans because of repeated exposure to harmless humans (Lowry et al. 2013; Møller et al. 2015; Uchida et al. 2019). This behavioral modification may minimize costs associated with responding to benign humans and permit coexistence with humans (Blumstein 2016). On the other hand, habituation may also make prey species more vulnerable to

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predatory threats (Geffroy et al. 2015). Therefore, behavioral modification in response to chronic human-induced stress is likely to have profound long-term individual fitness and population consequences (Blumstein 2016). Although many studies have assessed changes in tolerance in free-living animals, its mechanisms and long-term fitness consequences are not fully understood.

To properly study habituation and sensitization, individuals must be followed over time and over repeated exposures. This is relatively rare. For example, FID is one of the most widely used measurements to quantify behavioral responses to humans (Cooper and Blumstein 2015; Blumstein 2019). However, only a few of many thousands of FID studies have focused on individually marked animals (Runyan and Blumstein 2004; Carrete and Tella 2010; Petelle et al. 2013; Carrete et al. 2016). Continuous exposure to human disturbance may have a long-term effect on individual fitness and population dynamics, which is not able to be determined by a snapshot or a short-term study. Considering how wildlife behaviorally responds over time to chronic human disturbance may help us to draw better inferences about the long-term effects of human disturbance on the fitness consequence of wildlife.

Additionally, most prior studies have focused on quantifying a single behavior (most often FID) to detect changes in tolerance. Yet, we know that animals respond to threats in various ways and that antipredator responses are complex (Lima and Bednekoff 1999). Importantly, antipredator behaviors may have both different costs and different benefits. Therefore, to study the long-term ecological outcome of habituation and sensitization to humans, we must develop a more comprehensive framework by considering more than one behavior. For example, animals allocate time to scan for threats while foraging and then respond to threats by increasing their alertness and/or by escaping (Ydenberg and Dill 1986; Makowska and Kramer 2007). These behaviors reflect different aspects of predation risk management; time allocated to vigilance reflects the individual baseline vigilance levels to the ambient environment during foraging (Lima and Bednekoff 1999), whereas the decision to escape reflects the response to urgent threats, such as a predator approaching. Importantly, individuals may adjust these behaviors together or independently to compensate for the time and energy to allocate to foraging and reproduction (Cooper and Frederick 2007). There is therefore no a priori reason to expect that all antipredator behaviors respond the same way. This justifies considering more than one behavioral response and, by doing so, we will develop a more comprehensive understanding of the consequences of living with humans.

Here, we focused on yellow-bellied marmots, *Marmota flaviventris*, living in and around the Rocky Mountain Biological Laboratory (RMBL), Crested Butte, CO, as a mammalian model of habituation and sensitization. Marmots are common in Colorado's alpine and subalpine environments and are obligate hibernators (Armitage 2014). The marmots at the RMBL are an excellent system to evaluate the long-term impact of human disturbance on wildlife because they have been under continuous study since 1962 (Blumstein 2013; Amitage 2014). Individuals are identified to monitor behaviors, including antipredator (Runyan and Blumstein, 2004; Blumstein et al. 2008) and long-term demographic responses to environmental changes (Ozgul et al. 2010; Maldonado-Chaparro et al. 2018; Cordes et al. 2020; Paniw et al. 2020). Additionally, because the area around RMBL is the site of active outdoor recreation, and marmots may live near trails, roads, and cabins, marmots coexist with humans in a variety of areas subjected to different degrees of human exposure and hence impact (Li et al. 2011). Particularly, some colonies are located where researchers at the biological laboratory live during the

summer (details in Materials and Methods). Because marmots hibernate for about 7 months annually, they must concentrate growth and reproduction into their short summer active season (Armitage 1988). In short, changing the time allocation to foraging due to habituation or sensitization to humans may have a significant effect on mass gain because the degree to which animals can gain body mass during the summer season is a key element for overwinter survival (Armitage et al. 1976; Armitage 1988; Cordes et al. 2020).

We propose a simple framework to study the patterns of habituation and sensitization that compares individuals living in higher and lower disturbance areas. In this framework, we employ two common antipredator responses (vigilance while foraging and FID) and a fitness-related trait in our focal species—the rate at which individuals gain body mass during their active season—because this is likely to reflect a suite of risk assessment decisions. Vigilance while foraging is an important way that animals detect predators and estimate predation risk (Lima and Bednekoff 1999; Armitage and Salsbury 2016). Typically, foraging and vigilance are traded-off against each other: individuals forage less as they increase time allocated to vigilance (Lima 1987), resulting in less time to gain body mass. FID should reflect a marmot's perception of the approaching threat as well as its background risk assessment and may directly be associated with its tolerance to the approaching stimuli (Stankowich and Blumstein 2005; Samia et al. 2015). In short, if FID in response to humans changes over time, we can infer habituation or sensitization.

Differentiating the response to vigilance and FID is important because the outcome of interacting with humans may vary. While vigilance during foraging reflects the fundamental responsiveness to risk and is more directly related to fitness, FID is the direct measurement of habituation/sensitization to humans. Looking at both behavioral responses simultaneously may enable us to better infer the long-term effect on survival and fitness. Additionally, a recent paper suggested that changes in tolerance to humans influenced other antipredator behaviors in other threatening contexts (McCleery 2009; Geffroy et al. 2015). For example, habituation to humans due to nonthreatening interactions with humans may be associated with prey engaging in bolder activities and reducing their vigilance. We suggest possible outcomes when animals interact with humans in a habituation/sensitization framework and illustrate these in Figure 1. Scenario A-1: Animals comprehensively habituate to humans with decreased vigilance, indicating that habituation to humans is related to decreased baseline vigilance levels. In this case, vigilance and FID would decrease in highly disturbed areas with repeated exposure to humans, which is shown by the arrow in Figure 1. At the same time, the rate of body mass gain would increase in highly disturbed areas because exposure to humans modifies overall risk assessment and individuals would be able to allocate more time to foraging. Scenario A-2: Animals more selectively habituate to humans only, indicating that habituation would not influence vigilance. In this case, only FID might decrease in highly disturbed areas, whereas vigilance may remain either stable at the same level in low disturbance areas or potentially increase. The rate of body mass gain would be either consistent or decrease. Scenario B-1: Animals comprehensively sensitize to humans with increased vigilance, indicating that sensitization is related to the increased baseline vigilance levels. In this case, vigilance and FID would be increased in highly disturbed areas, whereas the body mass gain rate would decrease because they are less able to acquire resources and/or might be chronically stressed. Scenario B-2: Animals more selectively sensitize to humans only, indicating that sensitization to humans would not influence the vigilance. In this case, FID would

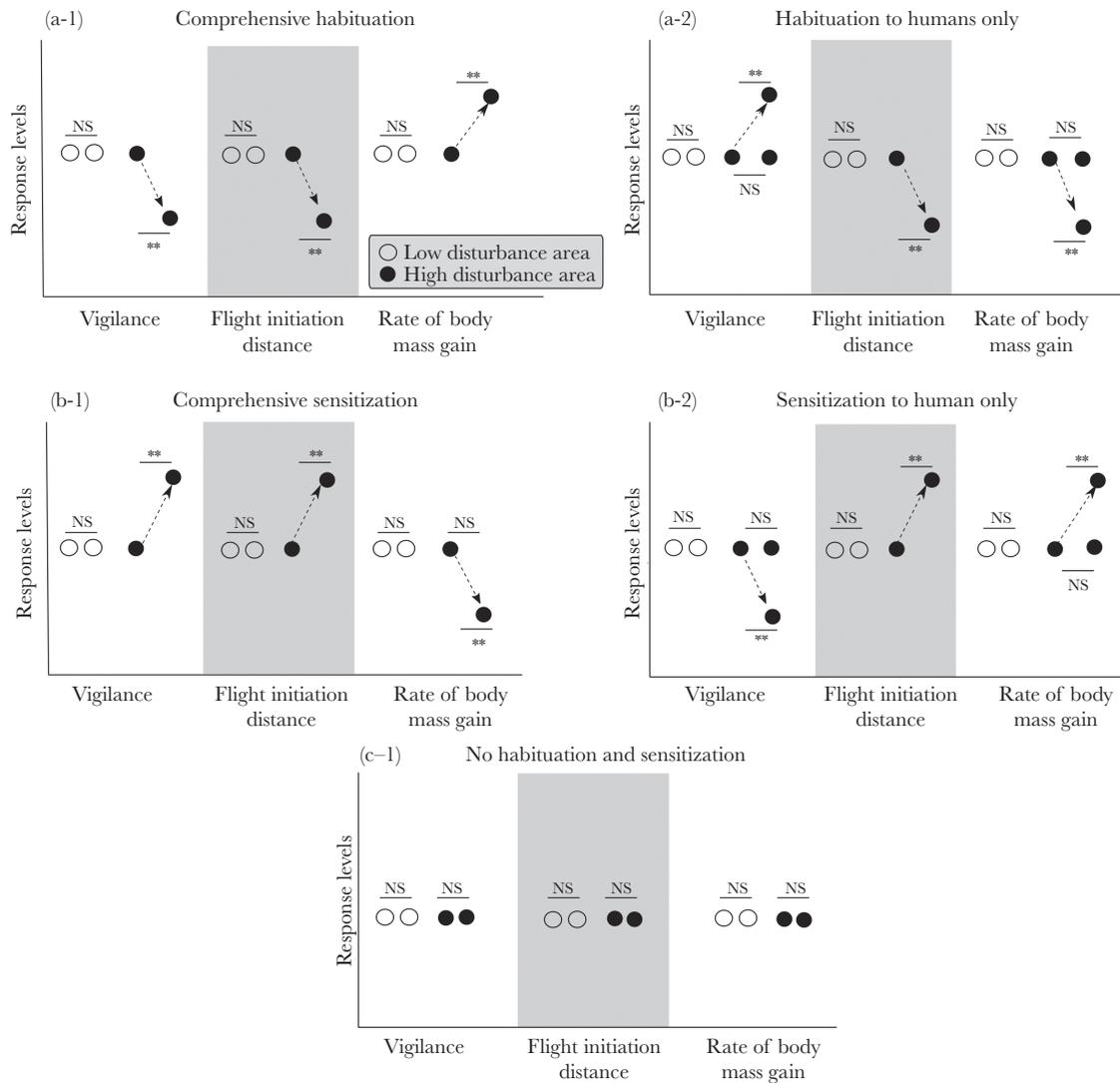


Figure 1

Possible scenarios illustrating habituation and sensitization to humans by animals in areas of high and low human disturbance (Scenarios A, B, and C). The x axis represents the two antipredator behaviors (individual time allocation to vigilance and flight initiation distance) and the rate of body mass gain (a trait correlated with fitness in yellow-bellied marmots). The y axis shows the relative magnitude of each variable. Low and high human disturbance levels are illustrated by white and black circles, respectively. Changes of two antipredator behaviors and the rate of body mass gain over time are shown by “**,” whereas “NS” represents that there is no change. Scenario A illustrates habituation to humans. (A-1): Animals comprehensively habituate to humans with decreased vigilance in the highly disturbed area. Vigilance and FID would decrease in highly disturbed areas with repeated exposure to humans, and individuals gain more body mass in highly disturbed areas than the ones in less disturbed areas. (A-2): Animals habituate to humans only. In this case, only FID might decrease over time, whereas vigilance may either increase or remain consistent. The rate of body mass gain would be either consistent or decrease. Scenario B illustrates sensitization. (B-1): Animals comprehensively sensitize to humans with increased vigilance. In this case, animals would increase vigilance and FID over time in a highly disturbed area, whereas the body mass gain rate would decrease. (B-2): Animals sensitize to humans only. Animals increase FID over time in a highly disturbed area, while vigilance would either decrease or remain consistent. The rate of body mass gain would either increase or remain consistent. Scenario C: Animals neither habituate nor sensitize. Vigilance and FID remain unchanged and there are no differences in the rate of body mass gain across a human disturbance gradient.

increase in highly disturbed areas, whereas the vigilance would either decrease or remain consistent at the same level in low disturbance areas. In this case, the rate of body mass gain would either increase or remain consistent. Scenario C: Animals neither habituate nor sensitize. Vigilance and FID remain unchanged and there are no differences in the rate of body mass gain across a human disturbance gradient. This might reflect that the gradient is not meaningful to the animals or that animals are not impacted by human disturbance.

We applied this predictive framework to marmots to understand the behavioral patterns and consequences of variation in long-term exposure to humans. To study the changes in human tolerance over time, we classified 11 marmot colonies into high and low human disturbance levels. Then, we used 15 years of marmot behavioral data to compare high and low disturbance areas in whether and how behaviors changed over time (vigilance and FID) as well as whether and how the rate of body mass gain during the summer changed over time to evaluate the fitness consequences

of long-term continuous exposure to humans. Using mixed-effect models, we asked whether year, disturbance level, and the interaction between year and disturbance level explained the variation in these antipredator behaviors and on the rate of body mass gain throughout the summer active season. We also assessed individual changes in tolerance toward repeated human approaches by determining whether the number of our experimental approaches influenced how individual marmots reacted to an actual human disturbance.

MATERIALS AND METHODS

Study area and animals

We studied marmots in the Upper East River Valley in and around the RMBL (38°57', -106°59'), Crested Butte, CO. During the marmot active season (mid-April through September), humans living in and around the RMBL townsites has been used by the scientific community since 1928. For decades, the Gothic population was capped at 160 people but, now, Gothic is home to 180 residents during the peak of the marmot active season with more researchers living offsite and commuting to Gothic for access to research facilities. Thus, we know that marmots have been exposed to human disturbance for more than 15 years and, by some measures (e.g., hotel occupancy rates in nearby Crested Butte and Mount Crested Butte have increased over time and summer tax revenues have increased over time), outdoor recreation (hiking and mountain biking during the summer; skiing and snowshoeing in the winter and spring) and research intensity (as measured by the number of approved research projects at the RMBL) are increasing, especially in highly disturbed areas. We chose 11 marmot colonies exposed to different degrees of human disturbance (Gothic Townsite, Horse Mound, Bench, Marmot Meadow, Picnic, River, River Annex, Avalanche, Boulder, North Picnic, and Stonefield). There are no continuous measures of human disturbance intensity for all sites (Li et al. 2011 only focused on a subset of these sites); thus, we categorized the intensity of human disturbance into two levels (high and low) based on the relative nature and intensity of human visitation. Highly disturbed colonies were those located near cabins, and where burrows were within 250 m of roads or well-used hiking trails (Gothic Townsite, Horse Mound, Avalanche, Bench, Marmot Meadow, Picnic, and River Annex). In these areas, marmots repeatedly encountered humans, mountain bikes, and vehicles. Colonies with low human disturbance were located farther away from human residential areas and roads/trails (River, Boulder, North Picnic, and Stonefield). We observed important marmot predators, including red foxes (*Vulpes vulpes*) and coyotes (*Canis latrans*), in both disturbance areas.

Marmots were routinely trapped and permanently identified using numbered ear tags and given unique fur mark for individual identification from afar (Blumstein 2013). Marmots spend more than 60% of their aboveground activity time scanning for conspecifics and predators (Armitage et al. 1996; Armitage and Salsbury 2016) and flee to their burrows when they detect threats. We focused specifically on the time marmots allocated to vigilance while actively engaged in foraging bouts (*sensu* Chmura et al., 2016).

Measuring the time allocated to vigilance while foraging

We quantified time allocated to vigilance during foraging bouts between May and September 2002 to 2018. During this period,

observers conducted 2-min focal observations on foraging marmots on most days during hours of peak activity (07:00 to 11:00 AM and 4:00 to 7:30 PM), weather permitting (Blumstein et al. 2004). We dictated into microcassette recorders the onset of foraging (stand forage and rear forage), vigilance (stand look and rear look), and locomotion (walk and run) and noted periods when focal individuals were out-of-sight behind rocks or vegetation. We transcribed focals using JWatcher 1.0 (Blumstein and Daniel 2007). To minimize observer bias, each observer was trained to identify behaviors with 100% accuracy and also trained with JWatcher until intraobserver scoring reliability was ≥ 0.95 . During the observation, we also recorded the factors that would influence vigilance, including the number of individuals within 10 m from the focal individual, and the distance to the nearest burrow (the distance at which focal individuals were initially observed). We included these covariates along with sex and age class (yearling and adult) in the statistical model.

Measuring FID

We estimated FID independently of vigilance. To do so, we measured FID in the field from 2003 to 2018 (no FID data were collected between 2006 and 2008). We trained observers to identify a target marmot, then walked directly toward the individual at a constant speed of 0.5 m/s, dropping flags at the points where they started the experimental approach (start distance), when the subject oriented its head toward the person (alert distance), and when the subject first began to move away from the approaching person (FID). We used a laser rangefinder (Yardagepro 400, Bushnell Performance Optics), or a meter tape, to measure three distances to the nearest 10 cm: starting distance (SD: the distance between the subject and person when the experimental approach began), alert distance (AD), and FID. We also recorded the distance to the nearest burrow, which was likely to influence FID. We included these covariates in statistical models. Most individuals were approached repeatedly on different days and some were approached twice on a single day (no more than once in the morning and once in the afternoon).

Body mass gain rate

Between 2003 and 2018, we attempted to catch each animal every other week. Each time an individual was captured, we recorded its body mass (to the nearest 50 g), sex, age, and reproductive status. We used these data and fitted a linear mixed-effect model to estimate the best linear unbiased predictors of body mass on 1 June and 15 August. The model had an individual identity, year, and colony included as random effects (Ozgul et al. 2010; Maldonado-Chaparro et al. 2015). Using these predicted values, we calculated, for each individual and each year, the daily rate of body mass gain. In this study, we focused on body mass measurements of yearlings (animals born the summer before who had survived their first hibernation) and adults (reproductively mature individuals that were ≥ 2 years old).

Statistical analysis

To test the effect of year and human disturbance level (high and low) on vigilance, FID, and body mass gain rate, we developed a series of mixed-effect models with the following dependent variables: the proportion of time in sight allocated to vigilance, FID, and the rate of body mass gain. Prior to fitting a model, all numeric variables were zero-centered, allowing us to compare the

effect size of each variable on the same scale. We also scaled and zero-centered the dependent variables so that we could compare among different models.

In the vigilance model, we used individuals with ≥ 3 focal observations to examine how vigilance changed over time and with more observations. Specifically, we fitted a random intercept and random slope model that permitted us to test whether individuals respond differently to repeated observation. We included year, disturbance level, the interaction between year and disturbance level, the number of individuals within 10 m, distance to burrow, sex, valley position (down-valley or up-valley), trial number (i.e., observation numbers on each individual), and age class (yearling and adult) as fixed effects. We also included individual ID as a random intercept and trial number as random slope to test whether there is individuality in vigilance change over repeated observations. If individuals changed their vigilance levels as the number of observations increased, the intercept (individual value of vigilance) and the slope of the trial number would be correlated. To test if the model with the random intercept and random slope was better than a random intercept model, we used a likelihood ratio test. Distance to burrow was \log_{10} -transformed. We included the valley position to acknowledge that there is an environmental difference between down-valley colonies and up-valley colonies that have demonstrable effects on marmot life-history traits, such as reproduction (Vuren and Armitage 1991), survival (Ozgul et al. 2006), and body mass (Ozgul et al. 2010). The day of snowmelt is about 2 weeks later in up-valley and marmots have less time to gain the body mass compared to conspecifics in down-valley (Armitage 2014). To simplify model interpretation, when control variables (the number of individuals within 10 m, distance to burrow, valley position, sex, and age) were not significant ($P > 0.05$), we removed them from the model and refitted the model.

In the FID model, we used individuals with ≥ 3 observations to study how FID changed over time and with more observations. We fitted a random intercept and random slope model for the same reasons explained above for the vigilance model. The starting distance, year, disturbance level, the interaction of year and disturbance level, distance to burrow, sex, valley position, trial number, and age class were included as fixed effects. Similar to our analysis of vigilance, we included individual ID as a random intercept and trial number as a random slope. The random intercept and random slope model enabled us to estimate the correlation between an individual's value of FID and the trial number, which permits us to quantify the individual variation of behavioral changes to repeated human disturbance. In short, a correlation between the intercept (i.e., the individual value of FID) and slope of trial number would help understand if those individuals with relatively high (or low) FIDs were more likely to increase or decrease FID over repeated experiments. If individuals differently changed their FID as an increased number of trials (i.e., they habituated or sensitized to humans), the intercept (individual value of FID) and the slope of the trial number will be correlated. To test if the model with random intercept and slope was better than a random intercept model, we used a likelihood ratio test. Metric measurements (SD, FID, and distance to burrow) were \log_{10} -transformed. To simplify the model, when control variables (distance to burrow, valley position, sex, and age) were not significant ($P > 0.05$), we removed them from the model and refitted the model.

In the rate of body mass gain model, fixed effects included year, disturbance level, the interaction of year and disturbance level, sex, valley position, and age. We included individual ID and colony ID as random effects in the random intercept model. To simplify the

model, when control variables (valley position, sex, and age) were not significant ($P > 0.05$), we removed them from the model and refitted the model.

Multicollinearity of each model was tested by variance inflation factor (VIF) in package "car" (Fox and Weisberg 2018); there was none ($VIF < 2.0$). We visually checked the residuals of final models to ensure that they approximated a normal distribution and that a q-q plot was roughly straight. Conditional and marginal R^2 values were calculated to check the goodness of fit of the models with and without the random effects (Nakagawa and Schielzeth 2013). Statistical analyses were carried out using R software, Version 3.6.1 (R Development Core Team 2019). All linear mixed-effects models were fitted using the package "lme4" (Bates et al. 2015) and significance evaluated using "lmerTest" (Kuznetsova et al. 2017) and R^2 values were calculated using "MuMIn" (Bartoń 2020) in R software.

RESULTS

Time allocation to vigilance

In total, we used 2532 observations from 316 focal individuals for the final model (225 from high and 91 from low disturbance areas). Age, sex, distance to burrow, and the number of individuals within 10 m were not significant and were thus removed from the final model (age, estimate = -0.147 , standard error [SE] = 0.077 , $P = 0.573$; sex, estimate = 0.089 , SE = 0.081 , $P = 0.272$; distance to burrow, estimate = -0.044 , SE = 0.030 , $P = 0.139$; the number of individuals within 10 m, estimate = -0.047 , SE = 0.030 , $P = 0.104$; Supplementary Table S1). The random intercept and slope model fit the data significantly better than the random intercept model ($\chi^2 = 9.316$, $P = 0.009$; Supplementary Table S2). The random effects explained a substantial amount of the total variation (marginal $R^2 = 0.108$, conditional $R^2 = 0.226$). Individuals in higher disturbance colonies significantly allocated more time to vigilance than individuals in less disturbed colonies (estimate = -0.336 , SE = 0.062 , $P < 0.001$; Figure 2a; Table 1), while effect of year on vigilance was not significant (estimate = 0.057 , SE = 0.031 , $P = 0.06$; Table 1). There was a significant interaction between year and disturbance level (estimate = 0.213 , SE = 0.058 , $P < 0.001$; Figure 2a). Therefore, marmots in the two different disturbance regimes had different patterns of changing the amount of time they allocated to vigilance as a function of human disturbance versus the duration of our study. Marmots in less disturbed areas allocated more time to vigilance compared to marmots in more highly disturbed areas (Figure 2a). Marmots did not change the time they allocated to vigilance as they were observed more (estimate = 0.008 , SE = 0.020 , $P = 0.685$; Table 1). Marmots in the lower part of the valley allocated more time to vigilance than those living up-valley (estimate = -0.708 , SE = 0.059 , $P < 0.001$; Table 1). The correlation between trial number and time allocated to vigilance was very slightly positive (Figure 3a; Table 1).

Flight initiation distance

We used 761 FID observations from 129 individuals (104 from high and 25 from low disturbance areas, respectively). Sex and age were not significant and were thus removed from the final model (sex, estimate = 0.089 , SE = 0.093 , $P = 0.338$; age, estimate = -0.092 , SE = 0.069 , $P = 0.183$; Supplementary Table S3). There was no significant difference between random intercept and slope model and random intercept model ($\chi^2 = 1375.6$, $P = 0.143$; Supplementary Table S2). However, because the random intercept and slope

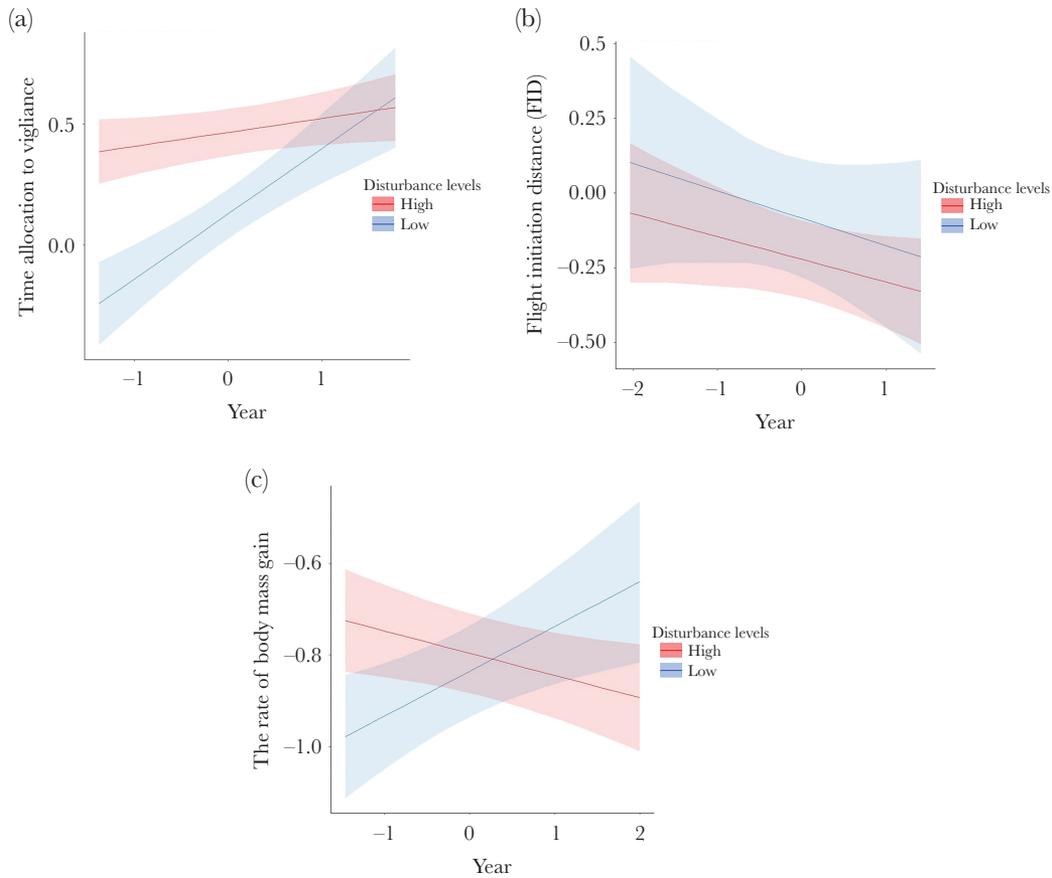


Figure 2

The relationships between each trait (a: time allocation to vigilance, b: FID, c: rate of body mass gain) and year/or disturbance level. Variables of time allocation to vigilance and the rate of body mass gain were standardized, and FID was also standardized after log₁₀ transformed. The lines represent the predicted probabilities from the linear mixed models with 95% CI of high and low colonies.

Table 1

The results of the linear mixed-effects model of time allocation to vigilance with random intercept and random slope. The R² of the model and random effects are also shown

	Estimate	SE	df	t value	P value
(Intercept)	0.462	0.049	342.635	9.366	<0.001
Year	0.057	0.031	346.540	1.866	0.063
Disturbance level: low	-0.336	0.062	429.221	-5.411	<0.001
Valley: up	-0.708	0.059	314.477	-11.949	<0.001
Trial number	0.008	0.020	867.782	0.406	0.685
Year × Disturbance level: low	0.213	0.058	592.169	3.662	<0.001
R ²	Marginal			Conditional	
	0.108			0.226	
Random effect		Variance	SD	Correlation	
ID	(Intercept)	0.112	0.335		
	Trial number	0.005	0.072	<0.01	
Residual		0.773	0.879		

Significant effects are shown in bold.

model provides more information than random intercept model, we interpret the results from this model. The random effects explained a substantial proportion of the variation in FID (marginal R² = 0.518, conditional R² = 0.717; Table 2). Marmots in highly disturbed areas tended to have shorter FIDs than those in less

disturbed areas (estimate = 0.170, SE = 0.10, P = 0.092; Figure 2b; Table 2) and marmot FIDs tended to decrease over study period, but the effects were not statistically significant. There was no interaction between year and disturbance level (estimate = -0.012, SE = 0.089, P = 0.894; Figure 2b; Table 2). However, trial number was

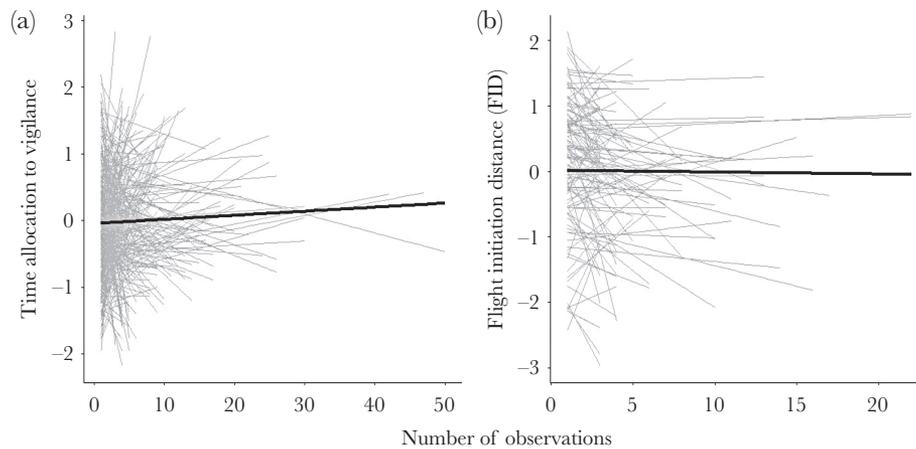


Figure 3

The time allocation to vigilance (a) and FID (b) of marmots across multiple observations. The bold lines are population average and each slope shows the average individual response to multiple observations.

Table 2

The results of a random slope and random intercept linear mixed-effects model explaining variation in FID. The R^2 of the model and random effects are also shown

	Estimate	SE	df	<i>t</i> value	<i>P</i> value
(Intercept)	-0.227	0.066	128.073	-3.427	<0.001
Year	-0.077	0.046	183.941	-1.662	0.098
Disturbance level: low	0.170	0.100	259.049	1.689	0.092
Start distance	0.506	0.032	532.779	16.034	<0.001
Distance to burrow	0.201	0.024	695.734	8.351	<0.001
Valley: up	0.360	0.092	130.074	3.928	<0.001
Trial number	-0.111	0.033	22.540	-3.394	0.003
Year × Disturbance level: low	-0.012	0.089	210.262	-0.133	0.894
R^2	Marginal			Conditional	
	0.518			0.717	
Random effect		Variance	SD	Correlation	
ID	(Intercept)	0.189	0.435		
	Trial number	0.006	0.076	0.73	
Residual		0.282	0.531		

Significant effects are shown in bold.

negatively associated with FID (estimate = -0.111, SE = 0.033, P = 0.003; **Figure 2b**; **Table 2**), showing that marmots, on average, tolerated significantly closer approaches the more times they were experimentally approached. The distance to burrow significantly explained the variation in FID (estimate = 0.201, SE = 0.024, P < 0.001; **Table 2**). Up-valley marmots had longer FIDs than down-valley marmots (estimate = 0.360, SE = 0.092, P < 0.001; **Table 2**). The individual's value of FID and trial number was positively correlated (r = 0.73, variance = 0.0006, SD = 0.076; **Figure 3b**; **Table 2**). Therefore, while marmots decreased FID ingeneral (as shown by significance of trial number as a fixed effect), individuals that have relatively longer value of FIDs, increased their FIDs with repeated trials throughout their lives and, hence, sensitized.

Body mass gain rate

We used 1446 observations from 728 individuals (499 from high and 229 from low disturbance areas). The conditional R^2 was

slightly higher than the marginal R^2 (marginal R^2 = 0.521, conditional R^2 = 0.549), suggesting that the random effects were relatively unimportant in explaining variation in the rate at which marmots gained body mass. We found that, on average, the rate of body mass gain during the summer has significantly decreased over 15 years (estimate = -0.044, SE = 0.022, P = 0.048; **Figure 2c**; **Table 3**). Additionally, while the effect of disturbance level alone was not significant (estimate = -0.039, SE = 0.048, P = 0.435; **Table 3**), the interaction between year and disturbance level was significant (estimate = 0.145, SE = 0.041, P < 0.001; **Table 3**), showing that patterns of the rate of body mass gain over time are different between high and low disturbance areas. While marmots in the less disturbed areas gained more mass throughout the study period, the marmots in the more disturbed area decreased their rate of body mass gain over time (**Figure 2c**). The effect of disturbance levels became significant when the effect of year was considered. Marmots in the higher part of the valley gained mass more quickly than up-valley marmots (estimate = 0.107, SE = 0.047, P = 0.049; **Table 3**). Males and yearlings gained more mass, on average,

Table 3

The results of the linear mixed-effects model explaining the seasonal mass gain rate. The R^2 of the model and random effects are also shown

	Estimate	SE	df	<i>t</i> value	<i>P</i> value
(Intercept)	-0.797	0.045	23.488	-17.899	<0.001
Year	-0.044	0.022	714.804	-1.978	0.048
Disturbance level: low	-0.039	0.048	9.145	-0.816	0.435
Sex: male	0.888	0.040	604.601	22.231	<0.001
Age: yearling	0.962	0.038	1400.531	25.375	<0.001
Valley: up	0.107	0.047	8.403	2.295	0.049
Year × Disturbance level: low	0.145	0.041	818.316	3.525	<0.001
R^2	Marginal			Conditional	
	0.521			0.549	
Random effects		Variance	SD		
ID	(Intercept)	0.027	0.164		
Colony ID	(Intercept)	0.001	0.034		
Residual		0.446	0.668		

Significant effects are shown in bold.

than females or adults (male vs. female, estimate = 0.888, SE = 0.040, $P < 0.001$; adult vs. yearling, estimate = 0.962, SE = 0.038, $P < 0.001$; Table 3).

DISCUSSION

Understanding the long-term behavioral response to humans, including their putative fitness consequences, is an important way that behavioral ecologists can contribute to wildlife conservation and management. Increased tolerance to human disturbance is one of the most observable behavioral responses of many animals living in human-modified environments (Lowry et al. 2013; Samia et al. 2015; Gotanda 2020). Nevertheless, some animals become sensitized to humans (Reimers et al. 2009; Blumstein, 2013), which may cause deleterious effects on fitness and influence population dynamics and ultimately population persistence.

Here, we showed that individual yellow-bellied marmots decreased their FIDs with increasing numbers of trials where observers directly approached them. Additionally, while not highly significant, marmots tended to tolerate closer approaches from humans over 15 years (as illustrated visually in Figure 2b; $0.05 < P < 0.1$; Table 2). At the same time, at the individual level, those individuals that had relatively high FIDs further increased their FIDs as they were continually approached and, thus, can be said to have sensitized (Figure 3). By contrast, marmots allocated more time to vigilance in highly disturbed colonies but, over time, increased vigilance in low disturbance areas as well (Table 1). The rate of body mass gain, a chosen proxy for fitness, varied with human disturbance levels: marmots gained less mass in highly disturbed areas than in less disturbed areas over time (Table 3). Taken together, while marmots habituated to humans as a function of repeated exposure to humans, long-term continuous human disturbances may have negative fitness consequences, indicating the pattern of Scenario A-2 in our predictive framework. The mere presence of humans was associated with behavioral modifications that may have consequences for marmot fitness and population dynamics.

The long-term nature of this study enabled us to better identify the impact of human activity on animals. Nevertheless, most studies still have not considered the long-term responses of free-living animals at individual and population scales. Although the effect over

15 years was relatively weak (the year was not highly significant), our study showed that, at the population level, yellow-bellied marmots tended to change their vigilance and FID over time. At the individual level, we found that as animals were experimentally approached more, FID decreased. Importantly, these tendencies of behavioral changes over time were accompanied by a decrease in the rate of body mass gain during the summer. Previous studies in this system illustrated the importance of body mass on hibernation (Armitage et al. 1976); individuals that gain more mass during the summer have a better chance of surviving the winter. This strongly indicates that repeated exposure to human disturbance is likely to negatively impact fitness. Both year and the interaction between year and disturbance level were significant in our model for the rate of body mass gain, whereas the effect of disturbance level alone was not significant. Most studies have simply compared the animals' responses to humans between disturbed and nondisturbed environments to detect the impact of human activities (Lowry et al. 2013). Our results suggest that a cross-sectional, snapshot study would be insufficient to gain a more comprehensive understanding of the impact of human activity and illustrates the strength of long-term analyses.

These results suggest the utility of our general framework to understand the mechanisms of habituation and sensitization to humans and its consequence in free-living animals. Yellow-bellied marmots habituated to our repeated FID trials and tended to habituate to long-term chronic human disturbance, a widely seen behavioral response that has been viewed as an adaptive response by animals to decrease the impact of human activity (Blumstein 2016). However, by considering the changes of vigilance and the rate of mass gain, we identified potentially negative effects of increased human exposure. Human activity may fundamentally change patterns of vigilance as seen in wild reindeer (Reimers et al. 2009), pronghorn *Antilocapra americana* (Berger et al. 1983), and some avian species (Blumstein 2013). The varied effects would not have been identified if we had only examined one dependent variable. Since FID and vigilance during foraging are the key behaviors that are related to managing predation risk and energy intake across a wide range of species, our predictive framework can be widely used to evaluate the impact of human disturbance on wildlife.

Even though animals generally reduce their FID as a function of human visitation (e.g., Samia et al. 2015), it does not necessarily mean that they are completely tolerant to human disturbances. For example, Eastern gray squirrels *Sciurus carolinensis* in Central Park in New York had different flight responses to different human activities, indicating that they were still sensitive to certain human behaviors (Bateman and Fleming 2014). Shutt et al. (2014) found that a habituated population of western lowland gorillas (*Gorilla gorilla gorilla*) had elevated physiological stress in response to human visitation. Furthermore, a previous study in our marmot system showed that marmots increased vigilance levels as they were exposed to more cars and bicycles (Li et al. 2011). Taken together, while humans may be perceived as low-risk stimuli to some extent, human activity is likely to impose some stresses and energetic costs on wildlife that may increase the vigilance level, which ultimately causes negative fitness consequences. Future, targeted studies are required to investigate the impact the various human activities on wildlife.

Our random intercept and slope model showed that individuals may habituate or sensitize differently, which may have important implications for conservation and management. The purposeful habituation is sometimes used in wildlife management to minimize the detrimental effect of human disturbance (Blumstein 2016; Shutt et al. 2014). Our results showed that even though individuals habituated on average to human disturbance at the population level, individuals with longer FIDs became more sensitized to humans over time, indicating that we should not expect all individuals to have identical responses to humans. In particular, wary individuals may be more likely to have reduced fitness. Therefore, wildlife managers must consider the risk of promoting habituation in such individuals. This study emphasizes the importance of studying animal responses over time at the individual level to properly understand constraints on management (Runyan and Blumstein 2004).

While the overall time allocation to vigilance has increased over time, the positive relationship between year and vigilance was weaker in highly disturbed areas compared to less disturbed areas. This is consistent with a human-shield effect (Berger 2007), whereby predators often avoid areas where human activity is high, which decreases the predation risk and makes prey species less vigilant. Whereas red foxes and raptors were seen at all colonies, coyotes the main predators on adult marmots were less common in the townsites (Waser et al. 2014). Future studies are required to test the human shield hypothesis.

Whether behavioral changes toward humans are the product of local adaptation or behavioral plasticity has been actively debated (Møller 2008; McCleery 2009; Lowry et al. 2013). Humans may act as selection pressure and may create novel evolutionary consequences. For example, Arroyo et al. (2017) showed that Montagu's harrier *Circus pygargus* increased their boldness and aggression toward humans over 19 years. Moreover, the variation in boldness was reduced as shy individuals disappeared in the population, a finding consistent with directional selection on boldness. Additionally, FIDs of urban burrowing owls *Athene cucularia* were significantly shorter than rural conspecifics and were highly consistent within individuals along with being heritable (Carrete and Tella 2013). This is consistent with local adaptation or personality-based habitat selection (Carrete and Tella 2017; Mueller et al. 2018). However, changes in fear responses to humans may arise via phenotypic plasticity (i.e., through habituation). In the case of

marmots, we showed that individual FIDs changed with increased exposure to humans as previous studies reported (Runyan and Blumstein 2004; Petelle et al. 2013). This suggests that plasticity is likely a key mechanism underlying changes in FID. Furthermore, while there is modest (but significant) heritable variation in marmot vigilance (Blumstein et al. 2010), we have no evidence that this trait has evolved. This may be expected given the state-dependent nature of vigilance (Chmura et al. 2016). We, therefore, suggest, but cannot assert, that behavioral plasticity may play a key role in the behavioral modification toward humans in these marmots. Future studies are required to rigorously differentiate these two underlying mechanisms.

Given the evidence that marmots reduced their FIDs with increasing exposure to humans, it is a little surprising that there was no strong effect of year and disturbance level. One explanation would be that marmots in less disturbed colonies had already recognized humans from afar and habituated to them. Or it could be an artifact of our trapping (which was more-or-less the same in both disturbed and less disturbed areas), which may have provided sufficient disturbance to eliminate these effects. Importantly, however, to include the largest sample size, we did not systematically quantify the number of human visitations in each colony; rather, we simply categorized disturbance degree into two levels. We know from Li et al. (2011) that marmot FID was differently influenced by the types of different human activities (hiking, motorized vehicles, and bicycles), suggesting that marmots could differentiate the risks of a variety of human activities. Future long-term studies that are based on more detailed estimates of the magnitude and type of human disturbance are warranted.

Conservation implications

The future will be characterized by increased human-wildlife interactions due to urbanization and increased outdoor recreation. Thus, our study has several implications for wildlife conservation and management. First, the significance of the effect of year and the interaction between year and disturbance level underscores the importance of looking at long-term responses of wildlife to better understand the impact of human disturbance. Second, a comprehensive assessment using more than one behavior and fitness-related traits provides a greater ability to understand the specific nature of the impact of human activities; all responses to humans may not be identical. Third, our predictive framework offers valuable information to guide management strategies. For example, if a focal species' response was (A-2) or (B-1) of our framework, there might be a need to create a buffer between humans and focal species or to regulate human visitation. Alternatively, if individuals who habituated to humans also increased their rate of body mass gain, intentional habituation may be useful (Shutt et al. 2014). However, whenever intentional habituation is used, it is important to understand whether this affects the response to real predators (Geffroy et al. 2015). With respect to marmots, despite living in highly disturbed areas, human activities may, nevertheless, cause negative consequences as illustrated by its effects on the rate of mass gain. By quantifying specific changes in behavioral patterns in response to specific human activities (e.g., Li et al. 2011), it should be possible to make concrete recommendations about how to selectively manage these human activities to reduce disturbance.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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