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How do humans impact yellow-bellied marmots?

An integrative analysis

A thesis submitted in partial satisfaction
of the requirements for the degree Master of Science
in Biology

by

Alyssa Marie Morgan

2019

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ABSTRACT OF THE THESIS

How do humans impact yellow-bellied marmots?

An integrative analysis

by

Alyssa Marie Morgan

Master of Science in Biology

University of California, Los Angeles, 2019

Professor Daniel T. Blumstein, Chair

While many studies document specific human impacts on the behaviour and physiological responses of wildlife to humans, most have focused on these responses independently and over relatively short periods of time, and few have examined fitness correlates of the response to humans. To address this limitation, we studied yellow-bellied marmots (*Marmota flaviventer*). We first quantified the rate that vehicles, pedestrians and bicycles passed marmot colonies. We then asked whether variation in these disturbances were associated with marmot physiological responses including neutrophil-lymphocyte ratios (NLR), and faecal glucocorticoid metabolites levels (FGM), behavioural responses including flight initiation distance (FID) and the time marmots allocated to foraging, and a key fitness correlate—the rate of mass gain. We focused on

two years (2009 and 2018) when we quantified human disturbance in detail to determine if and how the relationships changed over time. We found that the number of vehicles and pedestrians passing within 300 m of a marmot colony stayed relatively constant between years, while there was variation in bicycles passing by marmot colonies between 2009 and 2018. Despite similar length growing seasons, marmots at colonies that had more disturbances gained mass more rapidly in 2018 than in 2009. By examining a suite of physiological, behavioural and key fitness correlates, and how they changed over time our findings are consistent with the hypothesis that marmots became more tolerant of human disturbances. This provides promise for this population in dealing with inevitable increases in eco- and nature-based tourism.

The thesis of Alyssa Marie Morgan is approved.

Gregory F. Grether

Peter Nicholas Nonacs

Daniel T. Blumstein, Committee Chair

University of California, Los Angeles

2019

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1. Introduction

Human activity is responsible for as much as 85% of large species diversity lost from certain ecosystems (Garden et al., 2006; Ceballos et al., 2015), as many as 1 million species threatened with extinction (IPBES, 2019), and the newly named geological epoch of the Anthropocene (Steffen, 2007). It is now increasingly important to develop a comprehensive understanding of how species are influenced by anthropogenic disturbances. Particularly to better preserve biodiversity, human disturbance factors such as climate change, habitat loss, as well as direct disturbances need study (Vitousek et al., 1997).

A focal species' habitat selection (Gill et al., 2001) and overt behaviours such as decreased responsiveness to human activities (French et al., 2017) are traditional responses used to measure human disturbance. However, there may be other observable responses to human activities that may indicate disturbance (Hunninck et al., 2017; Müllner et al., 2004). For instance, marine iguanas (*Amblyrhynchus cristatus*) respond to a gradient of human disturbances with changes in a suite of endocrinological, immunological, and oxidative stress responses despite limited variation in their overt behavioural responses (French et al., 2017). Even ecotourism, a human activity that is traditionally viewed as less invasive, can cause individuals to engage in risk avoidance behaviour, thus interrupting critical activities for survival as well as creating stress responses for individuals (Geffroy et al., 2017).

Traditionally, the effects of anthropogenic disturbance on animals have been measured in three ways: 1) endocrinological or immunological changes (Vyas et al., 2016; French et al., 2010, 2017); 2) behavioural changes, such as flight initiation distance, and the time individuals allocate foraging (Frid and Dill, 2002) and 3) demographic changes quantified by studying survival (Ruhlen et al., 2003). Remarkably, most studies have looked at these responses in

isolation. Such a limiting view may either under- or over-estimate the consequences of anthropogenic disturbance (Geffroy et al., 2015). Examining these factors together, over extended periods of time, can lead to a more comprehensive understanding of human impact and therefore is crucial for proper conservation and management (Bateman and Fleming, 2017).

Disturbance may be viewed categorically (humans present or not) or continuously (varying levels of disturbance can create varying levels of response) (Shutt et al., 2014; French et al., 2017). Moreover, a single disturbance can create a cascade of different responses. Understanding how these responses interact, and whether responses are direct or indirect, is critical to develop a comprehensive understanding of disturbance. Fig. 1 illustrates a conceptual model that incorporates both direct and indirect responses to human disturbance.

The first potential response to disturbance is change in physiological responses due to stressors. Stress responses modulate an individual's ability to react to a stimulus and eventually return to a normal state; a process referred to as homeostasis (McEwen, 2005). When stress-related hormones (glucocorticoids) are released, systems that initiate growth or reproduction are inhibited to allocate energy for initiation of defense mechanisms, or escape (Geffroy et al., 2017). Acute stress can therefore be beneficial, but chronic stress can have negative physiological consequences on several physiological processes such as metabolic, cardiovascular, and immunological system function (Vyas et al., 2016). This can further alter behavioural processes leading to reduced population performance (Millspaugh et al., 2004).

Physiological responses to stressors are often quantified by changes in fecal glucocorticoid metabolites (FGMs) because it is a minimally invasive method (French et al., 2010; Tingvold et al., 2013; Hunninck et al., 2017), and variation in stress hormone levels may be associated with survival. For example, yellow-bellied marmots (*Marmota flaviventer*) with higher annual FGM

levels have significantly reduced over winter survival (Wey et al., 2015). Although FGM's may be a stress indicator for shorter time frames, when used in combination with the ratio of neutrophils to lymphocytes ratios, they indicate that stress is experienced over a longer time frame (Davis et al., 2008).

Animals may also directly modify behaviour in response to anthropogenic disturbance. For instance, animals exposed to disturbance may reduce the time they allocate to foraging or antipredator vigilance (Frid and Dill, 2002) or there may be differences in their flight initiation distance (Griffin et al., 2007). Changes in antipredator behavior may alter population dynamics (Frid and Dill, 2002). Altered physiological and behavioural changes may both affect an individual's fitness. For example, for hibernating species, mass gain, a key fitness correlate (Ozgul et al., 2010) can be affected by increased stress or decrease in time allocated foraging.

Habituation, a process that leads to decreased response to a stimulus with increased exposure, is an important factor when considering disturbance (Villanueva, 2012). Although this process is adaptive and can be beneficial, ensuring that individuals will not respond to harmless stimuli (Blumstein, 2016), it also has the potential to have negative consequences such as making individuals less vigilant and therefore more vulnerable to predatory threats (Geffroy et al., 2015). However some individuals do have the ability to learn to adjust to a disturbance

Finally, it is also equally important to categorise type of disturbance (e.g., biking, hiking, photography, etc.) because there is no *a priori* reason to expect that animals perceive all threats similarly (Müllner et al., 2004; French et al., 2017; Mainini et al., 1993). For example, waterfowl are more sensitive to disturbance from people/animals that are moving than those who are immobile (Davidson and Rothwell, 1993). Slower aircraft may be more disturbing than faster moving ones; helicopters have been shown to flush waterfowl at a greater distance than faster

moving fixed wing aircraft (Smit and Visser, 1993). Frequency of disturbance also may play a role as shown in Alpine marmots (*Marmota marmota*) which adjust their response to increased levels of hiker activity (Neuhaus and Mainini, 1998).

We evaluated the value of a comprehensive study of human disturbance by expanding on a more focused study conducted in 2009 (Li et al., 2011) on yellow-bellied marmots' responses to human disturbance in and around the Rocky Mountain Biological Laboratory. This population was ideally suited for this study because marmots live in colonies that have differing levels of exposure to humans which allowed us to easily quantify a gradient of disturbance levels. In 2018 we repeated the initial study and expanded the scope by adding additional measures of disturbance that encompassed measures of physiology, behaviour, and putative fitness correlates. We suspected that ecotourism increased in this region over the intervening 9 years and therefore predicted higher levels of disturbance in 2018. We also predicted that incorporating a suite of behavioral and physiological variables could lead to alternative results than those identified in 2009.

2. Methods

Marmots were trapped using Tomahawk livetraps baited with horse feed that were placed next to burrow entrances (Tomahawk Live Trap, Hazlehurst, WI). Once captured, individuals' mass, sex, age, and reproductive status were recorded. Hair samples were collected for genetic analysis, and up to 3 ml of blood sample was collected from the femoral vein for a suite of endocrinological and health measurements. We collected fecal samples when present. All marmots were individually marked with a pair of uniquely numbered ear tags and their dorsal fur was dyed for identification from afar (Blumstein, 2013). All colonies were observed during

morning and afternoon peak marmot activity hours. Relative predator abundance (e.g. Armenta et al., 2019) was calculated by taking frequency of predator sightings (a binary score of 0 or 1 if a predator was seen during observation period) and, for each colony and each year, calculating the proportion of observation sessions where a predator was sighted. From this each colony was given a relative predator abundance score. We used a median split to categorise each colony-year as either high (i.e. above the median split) or low (i.e. below the median split).

2.1 Human disturbance

Following Li et al. (2011), we measured human disturbance during the July peak of the summer tourist season. We defined three disturbances categories: total vehicles, pedestrians, and bicycles. We counted the number of passes of vehicles, pedestrians, and bicycles that passed within 300 m of a colony. We quantified these disturbances between 29 June and 14 July 2009 and between 1 and 23 July 2018—the peak of the tourist season--during hours when marmots were most active (07:00-11:00 and 16:00-18:00) daily except Saturdays. Colonies observed included Town, Marmot Meadow, North Picnic, Stonefield, and River. Only five colonies, Marmot Meadow, North Picnic, Picnic, Stonefield, and Town were observed both in 2009 and 2018, and therefore these were the colonies that we used to compare disturbance data between the two years.

Distances were categorised with respect to the location of main burrows at each colony. We originally separated light and heavy vehicles; defining light vehicles as any vehicle with no more than two-axles, including all-terrain vehicles (ATVs) and motorcycles. Heavy vehicles included any vehicles with more than two-axles, or a two-axle vehicle pulling a trailer with wheels. Since the majority of vehicles passing near marmot colonies were light vehicles, we combined these

categories and used total vehicles in subsequent analyses despite any differences in noise that they might have generated. Bicyclists were counted even if the rider was walking their bicycle. Pedestrians included anyone walking or running within 300 m of a marmot colony. Counts were based on the number of times the type of disturbance passed the colony; a single individual or vehicle could be counted multiple times if they passed back and forth during an observation session.

Between 2010 and 2018, the Crested Butte Chamber of Commerce counted the total number of visitors that stop into their visitor's center each day. Crested Butte is about 12 km from the closest studied marmot colony and is the base of much of the Upper East River Valley's tourism. We used the July data as an index of regional tourism.

2.2 Faecal glucocorticoid metabolites

Faecal samples were collected in traps or while animal was being handled, transferred into self-sealing plastic bags within ≤ 2 h of defecation. Faecal samples were kept on ice in the field and then stored at -20°C until hormones were extracted within 7 months of collection. We selected an individual's first sample collected in May, June and July for analysis. In addition, if an animal was trapped more than a single time in a bi-weekly trapping session, we selected the first trapping to prevent stress associated with trapping potentially elevating FGM levels. Details of extraction (Blumstein et al., 2006) and assay validation (Smith et al., 2012) are published elsewhere.

2.3 Neutrophil-lymphocyte ratios

We used a drop of blood to make a thin layer blood smear, dyed it with a Fisher Hema-3 Stat kit and counted the number of neutrophils, lymphocytes, monocytes, and basophils until 100 cells were scored or 30 min elapsed (Nouri and Blumstein, 2019). The number of neutrophils were then divided by number of lymphocytes for analysis.

2.4 Flight initiation distance

We experimentally walked at a constant trained pace (0.5 m/s) toward relaxed marmots to estimate flight initiation distance (FID) (Blumstein et al., 2004). Following a standardised protocol (Runyan and Blumstein, 2004), we recorded starting distance (distance between animal and the starting point), alert distance (distance between observer and animal when animal first looked at observer), and distance fled to burrow. In addition, we noted the incline the marmot was initially on, as well as type of substrate (dirt, talus, low vegetation, high vegetation). FID's were only collected on individuals that had not been tested within a 3-day period, as well as when wind speed was ≤ 3 on the Beaufort scale.

2.5 Time allocated to foraging

We quantified the proportion time marmots allocated to foraging during 2 min foraging focal animal samples. Observers used voice recorder and noted behavioural transitions from a standardised ethogram that contained the following behaviours; stand forage, stand look (all 4 legs on the ground), rear forage, rear look, run, out-of-sight, walk and other (Blumstein et al., 2004). Recordings were then scored using JWatcher 1.0 software (Blumstein and Daniel, 2007).

2.6 Mass gain rate

Body mass was recorded at each marmot capture between May and September. We used best linear unbiased predictors (BLUPS) to estimate body mass early in the season and later in the season. Body mass measurements were split into 3 age groups: juveniles, yearlings, and adults (i.e., those ≥ 2 years old) and estimated predicted mass on 1 June and 15 August using a mixed model (Maldonado-Chaparro et al., 2015).

2.7 Statistical analyses

All statistical analyses were conducted in R version 3.4.3 (R Core Team, 2017).

Spearman rank order correlation coefficients were used to determine correlation of each disturbance type across colony sites between 2009 and 2018. We fitted linear mixed models using lme4 (Bates et al., 2015) for NLR, FGM, foraging, and FID—all of which had repeated measures per year per individual. Multiple regression was used to model variation in mass gain rate because we only had a single measure per individual. We ensured that the residuals of each model followed an approximately normal distribution by examining frequency histograms and q-q plots. Time allocated to foraging and NLR values were log-10 transformed to improve distributions. For NLR, FGM, and foraging models we included as fixed factors: age class, sex, predator index, year, disturbance, and the interaction of year x disturbance. For FID we included as fixed factors: starting distance, incline, distance to burrow, age class, predator index, year, disturbance, and the interaction of year x disturbance. Marmot identity was included as a random effect in the NLR, FGM, FID, and foraging models to control for repeated measures of the same

individual. Plots of frequency histograms of residuals and q-q plots suggest that residuals from the models did not deviate substantially from normality.

3. Results

3.1 Human disturbance

Comparing disturbance at marmot colonies between 2009 and 2018 showed that the relative rank order between each colony of disturbance level remained identical across sites for total vehicle passes ($r = 1$, $p < 0.001$; Fig. 2), and the rate of pedestrian visits ($r = 1$; $p < 0.001$; Fig. 2). By contrast, there was limited variation in the rate of bicycle-associated disturbance in 2009 between each site and between years disturbance estimates were not correlated ($r = 0.22$; $p = 0.771$; Fig. 2). Despite our impression that there was an increase in tourism over time, according to visitation counts from the Crested Butte Chamber of Commerce between 2010 and 2018 (data were not available prior to 2010), there were no statistically significant changes in the number of visitors to the Crested Butte Visitor's Center ($r = -0.41$; $p = 0.27$; Fig. 3).

3.2 Physiological, behavioral and key fitness correlate response

Across both years, we had 181 measurements for NLR (across 84 individuals), 247 measurements for FGM (across 132 individuals), 302 measurements for FID (across 144 individuals), 478 measurements of time allocated to foraging (across 184 individuals), and 250 unique measurements of mass gain.

There were no significant main effects or interactions between years explaining variation in NLR as a function of any of the three quantified disturbance types (Table 1). We found a

significant interaction between some stimulus types and year that explained variation in FGM: marmots exposed to more vehicles in 2009 had higher FGM but in 2018 there was no relationship between FGM and variation in the rate of vehicle passes. In 2009 marmots had lower FGM levels as bicycles increased, but again, in 2018, there was no relationship between these variables. Marmots significantly foraged less with increases in vehicles and bicycles in 2009 but had no relationship between the variables in 2018. Time allocated to foraging decreased with pedestrian activity in 2009, as it did in 2018, but in 2018 values were consistently lower. We found no significant main effects or interactions of measured disturbance factors explaining variation in FID. Marmots gained mass more slowly as a function of increased vehicle and bicycle disturbance, but increased mass gain in 2018 as a function of these disturbances.

4. Discussion

We studied a suite of physiological, behavioural, and a trait that should be a strong fitness correlate, the rate of mass gain (Ozgul et al., 2010), in yellow-bellied marmots in response to three types of human activities near their colonies in two years (2009 and 2018) to study how marmot responses may have changed over time. At least two types of these activities have remained relatively constant across colonies between years. While we found that some physiological and behavioural responses changed over time, human disturbance appears to not be negatively impacting marmots in regard to a key fitness correlate—the rate that they gain mass during the summer. For all disturbance categories we saw a significant increase in mass gain rates in 2018 in comparison to 2009 suggesting that despite other ways marmots may be affected, the human impacts we quantified may not negatively impact marmots. In addition, we found that marmots had reduced FGM levels, a short-term indicator of stress, as well as increased time

allocated foraging in 2018 compared to 2009 as a function of vehicular disturbance. This too suggests increased tolerance.

Bicycle disturbances appear to be associated with different phenotypic responses than those associated with vehicles and pedestrians. As bicycle-related disturbance increased, FGM levels stabilised in 2018 (as opposed to decreasing in 2009), and time allocated foraging stabilised in 2018 (as opposed to increasing in 2009). From this study, we are not able to determine why we observed these physiological and behavioural differences with bicycles however it is plausible that marmots may perceive bicycles differently. For example, cougars (*Puma concolor*) are particularly sensitive to bicycles compared to other human disturbances (Markovchick-Nicholls et al., 2007). This sensitivity may be due to the nature of bicycle disturbances: they may approach quickly and quietly and may surprise animals. Another potential reason may be that we found no correlation between bicycle activity near marmot colonies across years. Potentially for marmots to become more tolerant of human activities, disturbance may need to stay relatively stable over time, or potentially not exceed a potential threshold, similar to the response shown in chimpanzees (*Pan troglodytes schweinfurthii*) which significantly increased vocalisations when exposed to an average of 6 or more tourists at a given time (Johns, 1996). Also, bicycle-related disturbances varied little in 2009, and across both years occurred at a much lower rate than pedestrians and vehicles. Perhaps this disturbance category was too inconsistent to be reliably studied. Regardless of the mechanism, further studies are required to understand why bicycles may generate different physiological, behavioural and demographic responses than other anthropogenic activities.

A pattern of tolerance can occur via individual assortment whereby individuals unable to cope with increased disturbance move away from disturbance areas while those able to cope stay

(Bejder et al., 2009). Marmots disperse as yearlings and those that do not remain in their natal group. Because we have no indication that dispersal is associated with tolerance to human disturbance, we infer that individual assortment does not explain this pattern of tolerance seen in our system.

Another mechanism of tolerance occurs when individuals exposed to a repeated disturbance of a non-threatening stimulus habituates to the specific stimulus (Rankin et al., 2009) and the pattern of tolerance we observed may suggest that individuals have habituated to human disturbances. There were no individual marmots studied in both 2009 and 2018. Thus, while we cannot assert that the seemingly increased tolerance to disturbance was a function of habituation, we know that marmots in this population have the ability to habituate to repeated human disturbance (Runyan and Blumstein, 2004; Petelle et al., 2013).

A shortcoming of this study is the limiting factor of only having two years to compare. We attempted to control for obscuring and potentially confounding factors by including age, sex, and predator index in our models, however we acknowledge a number of other factors may influence response to threats. Environmental changes between years may include the date that snow melts because this influences growing season length as well as the duration that marmots have time to gain mass (Kroeger et al., 2018). In 2009, the first date of recorded bare ground at the RMBL weather station was 11 May, whereas in 2018 it was 5 May, allowing potentially an extra week of time to gain mass. This extra 6 days was not much but may have permitted marmots more time to forage more and therefore gain more mass in 2018 compared to 2009. This could have modified rates of mass gain (Heissenberger et al., in revision) and thus could conceivably explain the interaction between year and disturbance type on our response variables.

Changes in how humans have used the Upper East River valley may explain the pattern of tolerance observed. For example, in 2008 a bus service was started to manage vehicular traffic in the valley and this was expanded in subsequent years. Furthermore, in the summer of 2016, camping was restricted to a single established campsite between 15 June and 15 August, which likely reduced potential disturbances to a few marmot colonies during a key time that marmots must gain sufficient mass to survive hibernation. Our results suggest that these ecotourism management strategies may have effectively managed disturbances and conceivably been ultimately beneficial to the marmots.

Animals that can tolerate human activities in circumstances where human disturbance is unavoidable will fare better than those that cannot. Purposeful habituation can be a useful tool for conservation and management (Blumstein, 2016). A previous study of human disturbance in this population (Li et al., 2011) showed that marmots were more vigilant and spent less time foraging. However, combining these previous findings with data also collected in 2018 as well as analyzing a key fitness correlate gives us greater perspective on how humans impact marmots. We now understand that disturbance (as we measured it) does not significantly affect FID and this result combined with our understanding of how time allocated to foraging has changed appears to suggest a pattern of increasing tolerance to human disturbance over time. This combined with increased rates of mass gain in 2018 illustrate a different picture of disturbance effects on this marmot population and suggests that marmots are tolerating disturbance in a way that is not negatively impacting their ability to gain mass and therefore potentially negatively impact their winter survival and reproductive success (Armitage, 2014).

Previous work has highlighted potential shortcomings of traditional study measuring human disturbance effects; from how animal responses are measured, interpreted, or the time scale used

to study them which may ultimately lead to misconceptions of how a population is responding (Bateman and Fleming, 2017). In efforts to address some of these concerns, we've applied a more integrative analysis which may be beneficial for future studies. Our results highlight the utility of evaluating an explicit conceptual model that explores a variety of responses to disturbance as well as studying these effects over time. Future studies may benefit from using a conceptual model that also explores the effect of disturbance on vital rates and population dynamics to develop an even more comprehensive understanding. By adopting a more comprehensive approach, both temporally and in number of measurements may allow for more insight into population dynamics and therefore allow for more informed conservation decisions to be made.

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Appendix

Table 1. Results from linear mixed effect models explaining variation in potential factors influenced by human disturbance quantified three ways: the rate (N/h) that motorised vehicles passed within 300 m of marmot colonies the rate the bicycles passed within 300 m of marmot colonies and the rate that pedestrians passed within 300 m of marmot colonies. The dependent variables included: NLR = neutrophil-lymphocyte ratios; FGM = fecal glucocorticoid metabolites; foraging = proportion of time allocated to foraging during 2 min focal animal samples; FID = flight initiation distance; and mass gain = the rate of mass gain between 1 June and 15 August.

NLR

Parameter	Total Vehicles			Bicycles			Pedestrians		
	Estimate	Std. Error	P-value	Estimate	Std. Error	P-value	Estimate	Std. Error	P-value
Intercept	0.249	0.082	0.003	0.053	0.358	0.882	0.021	0.003	<0.001
Sex male	< 0.001	0.033	0.995	< -0.001	0.033	0.992	0.003	0.003	0.913
Age class yearling	-0.157	0.032	<0.001	-0.156	0.032	<0.001	0.015	0.003	<0.001
Year 2018	0.162	0.089	0.074	0.368	0.36	0.311	0.021	0.003	<0.001
Disturbance	-0.002	0.002	0.489	0.021	0.052	0.691	<0.001	<0.001	0.409
Predator low	-0.042	0.033	0.206	-0.039	0.031	0.213	0.005	0.003	0.109
Year 2018* Disturbance	< 0.001	0.002	0.566	-0.023	0.053	0.656	<0.001	<0.001	0.914
FGM									
Intercept	56.22	7.723	<0.001	168.6	30.549	<0.001	74.924	4.61	<0.001
Sex male	-2.28	3.799	0.549	-2.42	3.877	0.534	-1.118	3.916	0.776
Age class juvenile	1.847	4.584	0.687	5.2	4.395	0.239	3.341	4.928	0.499
Age class yearling	-6.199	4.704	0.189	-6.054	4.784	0.208	-7.22	4.941	0.147
Year 2018	-52.328	9.159	<0.001	-162.42	31.08	<0.001	-73.526	4.82	<0.001
Disturbance	0.669	0.191	<0.001	-12.99	4.423	<0.001	0.114	0.058	0.051
Predator low	0.209	3.845	0.956	-3.809	3.858	0.325	4.026	4.577	0.38

Year 2018* disturbance	-0.673	0.213	0.002	12.747	4.580	0.006	-0.087	0.1	0.381
Foraging									
Intercept	0.027	0.016	<0.001	-0.212	0.062	<0.001	0.02	0.011	<0.001
Sex male	0.005	0.006	0.423	0.007	0.006	0.233	0.003	0.007	0.69
Age class juvenile	0.025	0.008	0.002	0.015	0.007	0.041	0.022	0.008	0.007
Age class yearling	0.048	0.008	0.563	0.008	0.008	0.28	0.002	0.009	0.777
Year 2018	0.007	<0.001	<0.001	0.364	0.063	<0.001	-0.022	<0.001	0.021
Disturbance	0.002	<0.001	<0.001	0.058	0.009	<0.001	-<0.001	0.001	0.002
Predator low	0.007	0.008	0.381	0.019	0.006	0.002	-8.431	0.01	0.392
Year 2018* disturbance	0.002	<0.001	<0.001	-0.057	0.009	<0.001	-<0.001	<0.001	0.723
FID									
Intercept	14.511	10.808	0.181	6.284	28.21	0.824	-1.088	6.805	0.873
Start Distance	0.366	0.039	<0.001	0.379	0.036	<0.001	0.405	0.036	<0.001
Incline	-0.106	0.069	0.129	-0.121	0.069	0.08	-0.123	0.0697	0.077
Distance burrow	0.55	0.161	<0.001	0.541	0.161	<0.001	0.572	0.162	<0.001
Age class juvenile	-5.133	4.216	0.226	-6.344	4.14	0.128	-5.542	4.14	0.183
Age class yearling	-1.77	3.938	0.654	-2.821	3.855	0.465	-1.491	3.83	0.697
Year 2018	-11.022	10.49	0.295	2.455	28.18	0.6	2.455	5.19	0.637
disturbance	-0.193	0.205	0.347	-0.099	4.238	0.981	0.067	0.06	0.272
Predator low	8.643	4.262	0.044	10.201	3.86	0.009	11.22	4.9	0.023

Year	0.204	0.213	0.338	1.83	4.268	0.669	-0.072	0.083	0.394
2018*disturbance									
Mass Gain									
Intercept	8.798	1.674	< 0.001	37.196	7.389	< 0.001	13.541	0.9	< 0.001
Sex male	2.367	0.68	< 0.001	2.166	0.714	0.002	2.645	0.643	< 0.001
Age class juvenile	1.429	0.825	0.085	2.293	0.845	0.007	1.147	0.779	0.142
Age class yearling	6.623	1.005	< 0.001	6.798	1.052	< 0.001	6.17	0.953	< 0.001
Year 2018	1.015	1.806	0.576	-24.589	7.362	< 0.001	-3.92	0.815	< 0.001
disturbance	0.205	0.039	< 0.001	-3.028	1.082	0.005	0.059	0.011	0.135
Predator low	-0.62	0.793	0.434	-2.51	0.759	0.001	1.159	0.773	< 0.001
Year 2018* disturbance	0.155	0.042	< 0.001	3.016	1.096	0.006	0.033	0.015	0.039

Figure 1: Varying pathways by which human disturbance may ultimately effect animal population dynamics

Figure 2. The rate (N/h) of specific human disturbances on yellow-bellied marmot colonies. a total vehicles; b bicycles; c pedestrians. Human disturbance was calculated as the number of passes within 300 m of a marmot colony per hour. Illustrated are Spearman rank order correlation coefficients and the associated p-values.

Figure 3. Visitors to the Crested Butte Chamber of Commerce Visitor's Center in July (2010 to 2018). Illustrated is the Spearman rank order correlation coefficient and the associated p-value.

Figure 4. Graph of human disturbances and marmots' response in 2009 (dashed line) and 2018 (continuous line.) Black outlined graphs illustrate statistically significant year x disturbance interactions. Detailed model results are presented in tables 1-5.

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