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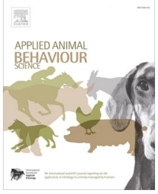

How do humans impact yellow-bellied marmots? An integrative analysis

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ABSTRACT

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. To address this, we studied a suite of responses in yellow-bellied marmots (*Marmota flaviventer*) in two distinct years, 9 years apart. We first quantified the rate that vehicles, pedestrians, and bicycles passed marmot colonies, focusing on two years (2009 and 2018) to determine how, if any of these relationships changed over time. We then asked whether these disturbances were associated with marmot physiological responses including neutrophil-lymphocyte ratios (NLR), and faecal glucocorticoid metabolites levels (FGM), as well as behavioural responses including flight initiation distance (FID) and the time marmots allocated to foraging, and finally a key fitness correlate—the rate of mass gain. 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. Despite similar length in growing seasons, marmots at colonies that had higher disturbance gained mass more rapidly in 2018 than in 2009. By examining a suite of physiological, behavioural, and key fitness correlates, and how they changed, our findings are consistent with the hypothesis that marmots became more tolerant of human disturbances over time. This provides promise for this population in dealing with inevitable increases in eco- and nature-based tourism.

1. Introduction

Human activity is responsible for as much as 85% of large species diversity loss from certain ecosystems (Garden et al., 2006; Ceballos et al., 2015) and 1 million species are threatened with extinction (IPBES, 2019). This has resulted in the newly named geological epoch of the Anthropocene (Steffen et al., 2007). It is increasingly important to develop a comprehensive understanding of how species are influenced by anthropogenic disturbances. To better preserve biodiversity, human disturbance factors such as climate change, habitat loss, as well as direct disturbances require in depth study (Vitousek et al., 1997). 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, 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 to vigilance or foraging (Frid and Dill, 2002; Gill et al., 2001) and 3) demographic changes quantified by studying survival (Ruhlen et al., 2003). Remarkably, most studies have looked at these responses in isolation from one another. Focused analyses may either under- or over-estimate the consequences of anthropogenic disturbance (Geffroy et al., 2015). 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).

Disturbance-induced endocrinological changes include stress responses which modulate an individual's ability to react to a stimulus (McEwen, 2005) through stress-related hormones (glucocorticoids) which trigger the "fight or flight" response (Geffroy, 2017). Acute stress can therefore be beneficial, but chronic stress can have negative

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consequences on several physiological processes such as metabolic, cardiovascular, and immunological system function (Vyas et al., 2016). Physiological responses to stressors are often quantified by changes in fecal glucocorticoid metabolites (FGMs) as it is a minimally invasive method (French et al., 2010; Tingvold et al., 2013; Hunninck et al., 2017). Neutrophil to lymphocyte ratios (NLR) are also an indicator of stress that is experienced over a longer time frame as stress hormones increase percentages of neutrophils and decrease percentages of lymphocytes (Davis et al., 2008). Given limitations of FGMs as an assessment of chronic stress without repeated measures, NLRs have been shown to be a reliable indicator of chronic stress in animals due to consistent haematological response (Davis et al., 2008; Swan and Hickman, 2014). Antipredator vigilance and decreased time allocated foraging are potential behavioural responses to anthropogenic disturbance (Frid and Dill, 2002), as well as differences in flight initiation distance (Griffin et al., 2007).

Both these immunological and behavioural responses may reduce survival and modify population dynamics. For example, yellow-bellied marmots (*Marmota flaviventer*) with higher annual FGM levels have significantly reduced over-winter survival (Wey et al., 2015). Changes in antipredator behaviour may lead to altered population dynamics (Frid and Dill, 2002) as well as physiological responses can further alter behavioural processes leading to reduced population performance (Millspaugh and Washburn, 2004). These responses may play a role in an individual's fitness and survival by effecting key fitness correlates. 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.

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, 2015). 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).

A meta-analysis (Bateman and Fleming, 2017) demonstrated that out of 102 studies on responses to ecotourism, only 5 studies used both a temporal and spatial experiment design. 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).

We evaluated the value of a comprehensive study of human disturbance by expanding on a study conducted in 2009 (Li et al., 2011) on yellow-bellied marmots' responses to human disturbance studied in the Upper East River Valley, near Crested Butte, Colorado. We suspected that ecotourism in this region has increased over the intervening 9 years and therefore predicted higher levels of disturbance in 2018. Based on results from 2009 that showed a relationship between marmot behaviour and human activity, we expected further modified behaviour as well as increased stress and decreased fitness with increases of disturbance over the 9 year period. This population was ideally suited for this study because marmots live in colonies with differing levels of exposure to humans which allowed us to evaluate a gradient of disturbance levels.

2. Methods

2.1. Study system

The study area is a 5 km portion of the Colorado East River Valley (38°57′N, 106°59′W) located at a 2900 m elevation. Marmot colonies are geographically distinct and dispersal between colonies is rare. Marmots were trapped using Tomahawk livetraps baited with horse feed 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 an 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).

2.2. Human disturbance

Following Li et al. (2011), we measured human disturbance at five marmot colonies during the peak of the summer tourist season (29 June and 14 July 2009, and 1 and 23 July 2018), during hours when marmots were most active (07:00–11:00 and 16:00–18:00) daily except Saturdays. We defined three disturbance categories: total vehicles, pedestrians, and bicycles. We counted the number of vehicles, pedestrians, and bicycles that passed within 300 m of a colony, distance between disturbance and colony were categorized with respect to the location of the main burrow. One marmot colony had a popular hiking trail passing within 300 m of the main burrow, which was included in our disturbance measurements. Bicyclists were counted even if the rider was walking their bicycle and pedestrians included anyone walking or running. 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.

2.3. Faecal glucocorticoid metabolites (FGM)

Faecal samples were collected in traps or while an 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., 2006a, 2006b) and assay validation (Smith et al., 2012) are published elsewhere.

2.4. Neutrophil-lymphocyte ratios (NLR)

In the field, we used a drop of blood to make a thin layer blood smear, dyed it with a Hema-3 Stat kit (Fisher Scientific, USA) 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.

2.5. Flight initiation distance (FID)

We walked at a constant trained pace (0.5 m/s) toward marmots not showing any sign of distress 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.

2.6. *Time allocated to foraging*

We quantified the proportion time marmots allocated 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 and analysed using JWatcher 1.0 software (Blumstein and Daniel, 2007).

2.7. *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 we estimated predicted mass on 1 June and 15 August using a mixed model (Maldonado-Chaparro et al., 2015). From these predicted values we estimated the daily mass gain (g/d) during the summer growing season.

2.8. *Statistical analyses*

We calculated Spearman rank order correlation coefficients to determine the correlation of each disturbance type across colony sites between 2009 and 2018. We fitted linear mixed models using lme4 (Bates et al., 2015) for dependent variables NLR, FGM, foraging, and FID—all of which had repeated measures per year per individual. We used multiple regressions 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. Whenever the interaction was non-significant, it was removed, and the model was recalculated (Engqvist, 2005). 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. Colony was included as a random effect for foraging and FID models but omitted from FGM and NLR models because we could not get models to converge properly with it included. All statistical analyses were conducted in R version 3.4.3 (R Core Team, 2017).

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. 1), and the rate of pedestrian visits ($r = 1$; $p < 0.001$; Fig. 1). By contrast, there was limited variation in the rate of bicycle-associated disturbance in 2009 between each site, and thus between years disturbance estimates were not correlated ($r = 0.22$; $p = 0.771$; Fig. 1).

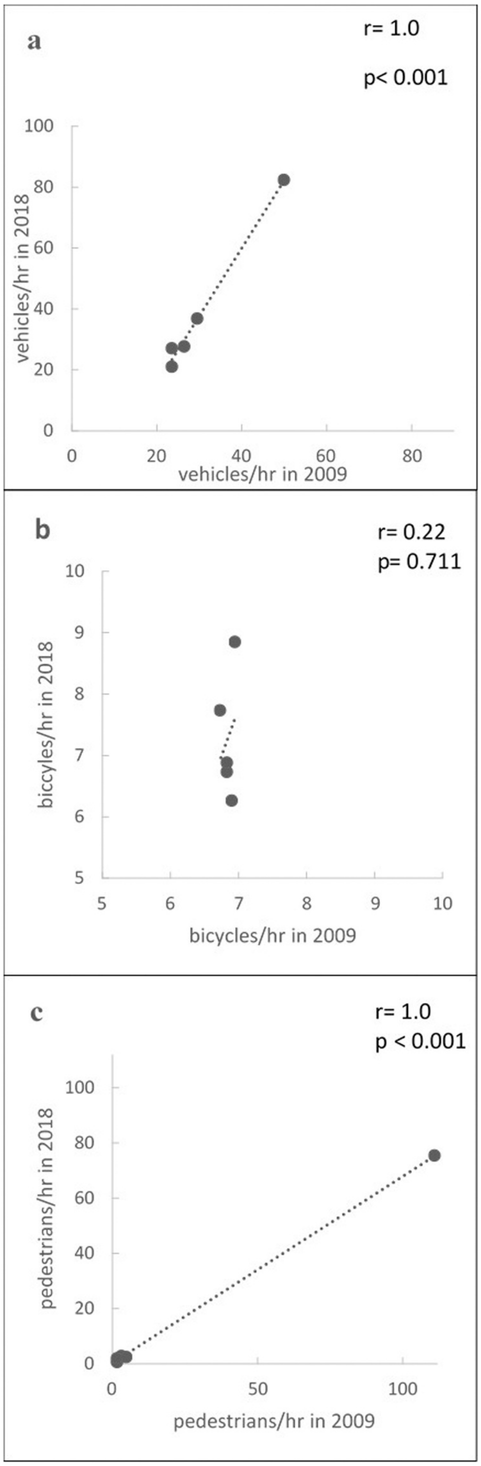

Fig. 1. The rate (N/h) of specific human disturbances on yellow-bellied marmot colonies. a total vehicles; b bicycles; c pedestrians. Human disturbance was calculated as the number of passes within 300 m of a marmot colony per hour. Illustrated are Spearman rank order correlation coefficients and the associated p-values.

3.2. *Physiological, behavioural and key fitness correlate response*

Across both years, we had 181 measurements for NLR (across 84 individuals) with a mean ratio of 1.14, 247 measurements for FGM (across 132 individuals) with a mean of 5.75 ng/g, 302 measurements for FID (across 144 individuals) with a mean flush of 32.51 m, 478 measurements of time allocated to foraging (across 184 individuals) with a mean forage proportion of 0.58, and 250 unique measurements of mass gain rate with a mean gain of 17.13 g/day. (Fig. 2).

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 more with increases in 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. 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 analyzed physiological and behavioural traits in yellow-bellied marmots in response to three types of human activities in two years (2009 and 2018) to study how marmot responses may have changed over time. While we found that some physiological and behavioural responses changed over time, human disturbance does not appear to negatively impact 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 compared to 2009. In addition, we found that marmots had lower levels of FGM, a short-term indicator of stress, as well as they spent more time foraging in 2018 compared to 2009 as a function of vehicular disturbance which also 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 stayed the same in 2018 (as opposed to decreasing in 2009), and time allocated foraging showed no effect in 2018 (as opposed to increasing in 2009). Bicycles are perceived differently in other animals; 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 not exceed a threshold, as it has been shown in other species (Johns, 1996). 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. Although we have no indication that dispersal is associated with variation in tolerance to human disturbance, future studies could investigate this in detail.

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). Similar patterns of tolerance have also been observed in another population of yellow-bellied marmots in Spokane, Washington when examining allostatic load in rural vs urban environments (Price et al., 2018). Price discovered a potential pattern of acclimatization where adults had lower levels of FGMs than juveniles or yearlings in response to urban environments, suggesting that age and potentially time exposed to a disturbance may allow for acclimatization and thus habituation (Price et al., 2018).

This study was limited by only looking at the effects of human disturbance across two years. We additionally 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 and therefore gain more mass in 2018 compared to 2009. This could have modified rates of mass gain (Heissenberger et al., 2020) and thus could conceivably explain the interaction between year and disturbance type on our response variables. Another limitation common when studying wildlife physiological and behavioral variables is sampling individuals via trapping. This iss its own form of disturbance that may be influencing response variables in our sampled population. However, our animals are trapped from birth and most trapping events are not physiologically stressful Smith et al. (2012)).

Changes in how humans have used the Upper East River valley between 2009 and 2018 may explain the pattern of tolerance observed. In 2008 a bus service was started to manage vehicular traffic in the valley and this was expanded in subsequent years, therefore potentially decreasing overall vehicular traffic. 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 visitor management strategies may have effectively managed disturbances and conceivably could contribute to this pattern of tolerance we have observed.

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 analysing 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 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). Our results highlight the utility of evaluating an approach 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

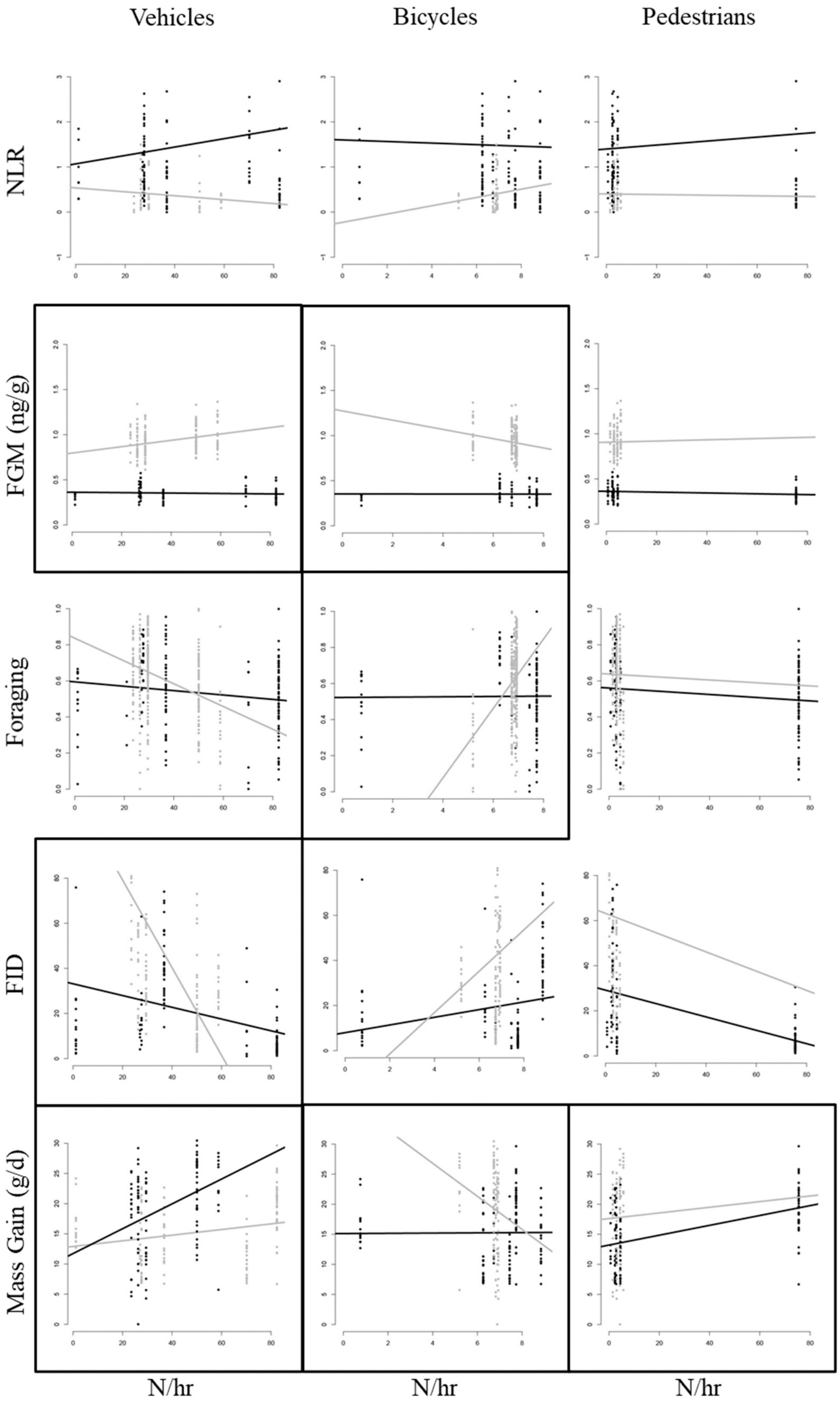

Fig. 2. Illustration of human disturbances and marmots' response including NLR (neutrophil-lymphocyte ratios), FGM (fecal glucocorticoid metabolites) in nanograms to grams (ng/g), foraging, and FID (flight initiation distance.) 2009 is illustrated in grey and 2018 illustrated in black. Black outlined graphs illustrate statistically significant year x disturbance interactions. Detailed model results are presented in Table 1.

Table 1

Results from 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. While mass gain rate results are from a linear regression, all other models were fitted as mixed effect models with marmot identity as a random effect. Illustrated are the fixed effects.

Neutrophil/lymphocyte Ratio									
	Total Vehicles			Bicycles			Pedestrians		
Parameter	Estimate	Std. Error	P-value	Estimate	Std. Error	P-value	Estimate	Std. Error	P-value
Intercept	0.209	0.044	**< 0.001**	0.21	0.069	**0.003**	0.213	0.036	**< 0.001**
Sex male	< 0.001	0.033	0.967	< −0.001	0.033	0.997	-0.003	0.033	0.905
Age class yearling	-0.155	0.032	**< 0.001**	-0.156	0.032	**< 0.001**	-0.151	0.032	**< 0.001**
Year 2018	0.209	0.033	**< 0.001**	0.207	0.032	**< 0.001**	0.204	0.032	**< 0.001**
Disturbance	< −0.001	< 0.001	0.65	-0.002	0.009	0.806	< −0.001	< 0.001	0.307
Predator low	-0.046	0.033	0.165	-0.041	0.031	0.181	0.055	0.034	0.104
Faecal Glucocorticoid Metabolites									
Intercept	56.22	7.723	**< 0.001**	168.6	30.549	**< 0.001**	7.504	0.77	**< 0.001**
Sex male	-2.28	3.799	0.549	-2.42	3.877	0.534	-0.154	0.388	0.692
Age class juvenile	1.847	4.584	0.687	5.2	4.395	0.239	0.218	0.491	0.658
Age class yearling	-6.199	4.704	0.189	-6.054	4.784	0.208	-0.82	0.49	0.096
Year 2018	-52.328	9.159	**< 0.001**	-162.42	31.08	**< 0.001**	-6.337	0.438	**< 0.001**
Disturbance	0.669	0.191	**< 0.001**	-12.99	4.423	**< 0.001**	0.27	0.01	0.27
Predator low	0.209	3.845	0.956	-3.809	3.858	0.325	0.47	0.8	0.468
Year 2018 * disturbance	-0.673	0.213	**0.002**	12.747	4.580	**0.006**	N/A	N/A	N/A
Foraging									
Intercept	0.233	0.032	**< 0.001**	-0.193	0.107	0.142	0.183	0.029	**< 0.001**
Sex male	0.007	0.006	0.293	0.007	0.006	0.248	0.007	0.006	0.271
Age class juvenile	0.024	0.008	**0.002**	0.022	0.008	**0.005**	0.024	0.008	**0.002**
Age class yearling	0.007	0.008	0.424	0.007	0.008	0.388	0.006	0.008	0.443
Year 2018	-0.013	0.009	0.172	0.35	0.104	**0.025**	-0.018	0.009	**0.047**
Disturbance	-0.001	< 0.001	0.067	0.054	0.016	**0.023**	-< 0.001	< 0.001	0.637
Predator low	-0.018	0.024	0.494	0.024	0.015	0.213	0.004	0.031	0.892
Year 2018 * disturbance	N/A	N/A	N/A	-0.054	0.015	**0.019**	N/A	N/A	N/A
Flight Initiation Distance									
Intercept	-39.417	33.635	0.275	-40.798	16.906	0.048	-31.79	18.41	0.115
Start Distance	0.344	0.035	**< 0.001**	0.303	0.035	**< 0.001**	0.34	0.035	**< 0.001**
Incline	-0.042	0.066	0.524	-0.029	0.066	0.661	-0.041	0.066	0.532
Distance burrow	0.623	0.149	**< 0.001**	0.549	0.15	**< 0.001**	0.615	0.149	**< 0.001**
Age class juvenile	-5.922	3.061	0.056	-6.169	3.379	0.07	-6.015	3.078	0.053
Age class yearling	-3.103	2.755	0.264	-2.945	3.094	0.344	-3.088	2.773	0.27
Year 2018	63.044	15.092	**< 0.001**	-4.393	4.448	0.33	24.005	5.054	**< 0.001**
disturbance	0.098	0.782	0.249	7.284	2.184	**0.013**	0.802	0.157	**< 0.001**
Predator low	9.302	22.079	0.686	26.475	12.527	0.087	34.275	21.346	0.149
Year 2018 *disturbance	-1.215	0.477	**0.026**	N/A	N/A	N/A	N/A	N/A	N/A
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**

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.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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