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ORIGINAL RESEARCH

Take only pictures, leave only… Cameras influence marmot vigilance but not perceptions of risk

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Abstract

Ecotourism provides an opportunity to experience nature that may promote its conservation. Ecotourists photograph wildlife, and photography plays an important role in focusing public's attention on nature. Although photography is believed to be a low-impact activity, how the visual stimulus of cameras influences wildlife remains unknown. Since animals are known to fear eyes pointed towards them because of similarity to predator eyes, we predicted that cameras with zoom lens would increase vigilance. Using yellow-bellied marmots (*Marmota flaviventer*) and adopting a behavioural approach to identify marmots' response to photography, we experimentally quantified proportion of time allocated to vigilance during foraging and flight initiation distance (FID, the distance at which a marmot started to flee from an approaching human) towards humans with and without a camera. We focused on time allocated to vigilance measured in three ways: the proportion of time when marmots moved their head and body towards observers (looking towards observer), the proportion of time when marmots moved their head away from observers (looking away from observer) and the total vigilance (sum of looking towards and away from observer). While a camera was pointed at a marmot, individuals allocated more time to looking towards the observer and less time to looking away from the observer than they did without a camera. However, the total proportion of time allocated to vigilance was not different when marmots were approached by humans with and without a camera. Additionally, whether or not an observer was carrying a camera had no effect on FID. Our results indicated that cameras distracted marmots but did not influence their subsequent risk assessment; marmots may be curious about cameras but were not threatened by them. However, capturing an individual's attention may reduce their ability to look out for predators and thus may increase vulnerability to predation. Regulating photography in locations where predation risk is high or vulnerable species ranges' overlap with humans may be required.

Introduction

Ecotourism is becoming increasingly popular as more people venture into protected areas. In 2019, 327.5 million people visited national parks in the US (National Weather Service, 2021). Ecotourism such as wildlife tourism has a positive effect on biodiversity conservation and human well-being. For example, wildlife tourism often produces financial benefits to local communities by making profits on nature-based tourism, which becomes an important incentive for local communities to create conservation areas (Sekercioglu, 2002). It also increases opportunities for people to experience nature, which may enhance conservation concerns (Soga & Gaston, 2020). However, since humans have been regarded as a super-predator (Darimont et al., 2015), and most animals are sensitive to human presence, increasing human visitation due to ecotourism likely has negative effects on animals' behaviours such as vigilance, foraging, mating and social interactions, which ultimately influence reproduction and survival. For example, wildlife living in human-visited areas are more physiologically stressed than individuals in areas not visited by humans (Geffroy et al., 2017). Prior studies have also shown that the presence of humans influences reproductive success and growth rate in California sea lions (*Zalophus californianus*; French et al., 2011). Common dolphins (*Delphinus delphis*) forage significantly less when disturbed by boats, which affects sociality and survival rate (Meissner et al., 2015). The by-products of ecotourism could, therefore, be potentially harmful. With an influx of ecotourists along with ever-decreasing biodiversity, the importance of comprehensively understanding human impacts is required for conservation. This requires the application of the tools of ethology and behavioural ecology, such as quantifying the behavioural responses to human disturbances in order to develop a fundamental understanding of how stimuli derived from human presence are perceived, and how they influence animal behaviour.

Human presence often increases vigilance in many animals (Clinchy et al., 2016; Reimers et al., 2009), which may impact reproductive success, somatic growth rate and survival rate. Since time allocated to vigilance is traded off with other fitness-related activities such as foraging and reproduction (Lima, 1987), increased time allocation to vigilance due to human disturbance would affect the individual opportunity for foraging and reproduction, which may decrease individuals' fitness. For example, wildlife tourists increase the frequency and duration of vigilance in the endangered, red-crowned crane (*Grus japonensis*; Li et al., 2011). Yellow-bellied marmots (*Marmota flaviventer*) in highly disturbed areas allocated more time to vigilance and had a lower rate of seasonal mass gain over time, which might be due to less time for foraging (Uchida & Blumstein, 2021). Understanding how human activities modify vigilance is essential for developing effective management actions to minimize human impacts on wildlife vigilance.

Wildlife photography has become one of the most common ecotourism-related activities with the technological development of cameras and the increased popularity of social network services (Ellenberg, 2017; Pagel et al., 2020). The common phrase, 'take nothing but photos, and leave nothing but footprints' makes the assumption that photography has no impact on animal behaviour, but the fact remains that we still do not fully understand the effect of photography on wildlife. Previous studies on female crested anoles (*Anolis cristatellus*) showed that the magnitude of response to shutter noises was about the same as that to predator calls (Huang et al., 2011). In addition to the shutter noise, photography may have another effect. For example, photographers approach animals while holding a camera with a huge zoom lens directed at animals. Generally, many species have an innate fear of eyes, with butterflies and caterpillars evolving eyespot patterns that reduce predation (Monteiro, 2015). From an individual prey's perspective, a camera lens may resemble the eye of a large predator. Although auditory and visual cues associated with photography in free-living animals have been studied together, the response to visual cues alone of a camera and a zoom lens has not been examined. Indeed, animals often use the cue of eyes pointed towards them to assess predation risk and many species respond aversively to even simulated eyespots. Bateman and Fleming (2014) reported that eastern grey squirrels (*Sciurus carolinensis*) in New York City escaped farther when approached by humans that looked at them compared to when individuals were not looked at. This suggested that individuals felt more at risk when they were stared at. With the popularity of wildlife photography (Fennell & Yazdan Panah, 2020) combined with relatively affordable large zoom lenses, it is increasingly important to know whether camera lenses evoke potentially fearful eyespot-like responses.

This study aimed to test whether a human with a camera influenced wildlife vigilance. In this study, we used yellow-bellied marmots in and around Rocky Mountain Biological Laboratory (hereafter, RMBL) in Gothic Colorado, USA, as a mammalian model. Marmots are an ideal mammalian model system to study the effect of cameras on behaviour because prior field studies have documented marmot antipredator behaviour in detail. Previous studies also showed that marmots detect predatory cues using olfactory (Blumstein, Barrow, & Luterra, 2008), acoustic (Blumstein, Cooley, et al., 2008) and visual modalities (Bednekoff & Blumstein, 2009; Blumstein et al., 2009). Due to their well-studied antipredator behaviour, marmots have been used to study the effect of human activity on vigilance behaviours and risk assessment (Li et al., 2011; Uchida & Blumstein, 2021). Additionally, the long-term human disturbance has modified marmots' vigilance behaviour and risk assessment towards humans (Morgan et al., 2021; Uchida & Blumstein, 2021). To test whether marmots increased vigilance in response to the visual presence of cameras, we approached marmots until they visually responded to the observer by looking towards them and then either pointed a camera with a zoom lens at them or simply looked at them while conducting a 1 min focal behavioural observation. Following the focal behavioural observation, we continued walking towards the subject until it fled and quantified flight initiation distance (the distance at which individuals start to flee from an approaching human, FID) and a measure of risk assessment. We expected that marmots would increase their perceptions of risk when a human pointed a large zoom lens directly at them. Thus, we predicted that marmots approached with a camera would increase their time allocation to vigilance and increase their FID compared with approaches without a camera.

Materials and methods

Marmots were studied between 15 June and 11 July 2021 in the East River Valley in and around the RMBL (38°57′, −106°59′). The upper East River Valley is a destination for outdoor activities (e.g. hikers, mountain bikers and photographers in the summer; skiers and snowshoers in the winter). Marmots are active between mid-April and late September which coincides with peak summer visitation. Following Uchida and Blumstein (2021), we observed marmots at 7 colonies (geographically distinctive locations containing one or more matrilines–Armitage, 2014). We focused on colonies with semi-regular human contact which we defined here as those within 250 m of hiking trails, dirt roads and cabins. All subjects were live trapped regularly and marked with unique ear tags and fur marks to identify individuals from afar (Blumstein, 2013).

Quantifying the response to a camera

To quantify marmots' behavioural responses to cameras, we approached them systematically with and without a camera. We targeted adult and yearling marmots that were initially relaxed (i.e. they were not looking at us and were either sitting, standing, lying down or foraging). Each individual was identified by its fur mark before initiating an experiment. We used a counterbalanced design which entailed alternating a camera presentation (i.e. approaching with a camera) and control presentations (i.e. approaching without a camera) for each new marmot tested. Each individual was approached with either experimental treatment (camera or control) at the first trial; then, they were given the other treatment for a second trial.

A single observer walked directly towards the target marmot at a constant speed of 0.5 m/s on a direct trajectory, stopping at the alert distance (hereafter, AD) where the animal looked at the person. At AD, the observer stopped walking and presented the treatment or control. The experimental treatment comprised of holding a camera at eye level that was directly pointed towards the target individual (with a camera), or, as a control, the observer simply looked directly at the marmot. For the next 60 s, we observed and quietly recorded the following behavioural transitions: 'rear look away from the observer' (individual stood bipedally with its head and body pointing away from observer to look around the surroundings), 'stand look away from the observer' (individual stood quadrupedally with its head and body pointing away from observer to look around the surroundings), 'rear look towards the observer' (individual stood bipedally with its head and body pointed towards observer) and 'stand look towards the observer' (individual stood quadrupedally with its head and body pointing towards the observer), and out of sight. Although we also recorded several non-vigilance behaviours (walk, run, stand and forage, rear and forage, self-groom and social interactions), we did not formally analyse them. After conducting the focal observation and recording the behaviours, the observer took the camera away from their eye and let it hang from its strap, and then resumed walking (at 0.5 m/s) towards the subject (if it was still there) until it flushed. When the target individual flushed, we measured the distance between observer and the point where the target individual was initially positioned at the flight initiation distance (Cooper & Blumstein, 2015). We also measured the initial distance between the target individual and the point where the observer started approaching, namely starting distance (hereafter, SD), which is known to influence AD and FID (Cooper & Blumstein, 2015). If an individual flushed before a behavioural focal could be started, then the experiment was terminated and we tried to study that subject on a different day. However, if an individual permitted at least 15 s of behavioural observations in a focal before flushing, we included the data (this happened twice). In these two observations, the FID was the same distance as the AD because the animal alerted to us and fled from us at the same distance.

We used two different cameras (Canon EOS7D mark2 and Pentax KP) with 13 cm wide bodies, 24–105 mm lenses for Canon and 55–300 mm lenses for Pentax which were ca. 20 cm long and 8 cm in diameter making them easily identifiable. Both cameras were similar in terms of size of lens and colour. All distances were measured using a laser rangefinder (Yardagepro 400, Bushnell Performance Optics, Overland Park, Kansas), or a meter tape to the nearest cm. An individual was not approached more than a single time in a given day.

Statistical analysis

We analysed four behavioural responses to the experimental treatments. First, we combined 'rear look towards the observer' and 'stand look towards the observer' to calculate the proportion of time (that a marmot was in sight) that it allocated to looking towards observer because we thought this would reflect specific vigilance directed towards humans. Second, we combined 'rear look away from the observer' and 'stand look away from the observer' to calculate the proportion of time allocated to looking away from the observer because we thought that this would reflect the individual wariness to non-human threats – such as predators and conspecifics. If we found that marmots spent more time looking towards observers with a camera directed at them compared with the control, it would suggest that the camera increased their vigilance. Third, we also focused on total vigilance (the sum of looking towards and looking away from the observer) because by being more vigilant, animals were unable to engage in other important activities, such as foraging. We divided the 60 s observations into 4 intervals (0–15 s, 15–30 s, 30–45 s and 45–60 s) to examine how each behaviour changed over time to detect short-term changes of risk assessment. Animals may either habituate or sensitize when individuals are repeatedly exposed to a stimulus, and previous studies showed that marmots decreased responsiveness to the repeated human approaches, indicating habituation (Runyan & Blumstein, 2004). If marmots decreased the proportion of time allocated to vigilance and looking at or away, it would indicate habituation to the experimental treatment. Finally, we measured FID after we quantified vigilance to examine how a camera presentation influenced marmot risk assessment.

We conducted 119 field experiments in total on 57 individuals. We excluded data from the statistical analysis when the individual flushed at AD (i.e. AD = FID) because we were unable to obtain any vigilance and FID observations. Although we initially fitted linear mixed effect models, the residuals of these models deviated substantially from normality and we could not transform variables to meet distributional assumptions (more details are in the Appendix S1). Therefore, we used permutation tests (with 1000 simulations) to study the effect of cameras on time allocated to vigilance. The permutation test permitted us to analyse the data given that its distribution deviated substantially from normality. We included the proportion of time allocated to total vigilance, looking towards the observer and looking away from the observer as dependent variables with individual ID as a random effect in each model. We also included the alert distance (AD), experimental treatment (camera presentation or control), time interval, sex, age class (adult or yearling) and the interaction between experimental treatment and time interval as independent variables and included as fixed effects.

We fitted a linear mixed effect model to examine whether variation in FID was explained by the experimental treatments (i.e. camera presentation or control). Log-transformed FID was included as a dependent variable and individual ID was included as a random effect. We initially also included colony ID as a random effect, but the model would not converge, so we removed it as a random effect. The log-transformed alert distance, experimental treatment (camera presentation or control), the total proportion of time the subject looked towards the person during the focal, sex, age class (adult or yearling), the interaction between experimental treatment and alert distance, and the interaction between experimental treatment and age class were included as fixed effects. To test assumptions of the mixed models, we visually checked the residual distribution of the FID models and they were approximately normal and the q-q plots were mostly straight.

We used R software, Version 3.6.1 (R Development Core Team, 2020), for all statistical analyses. We used the package named 'minque' for the permutation test (Wu, 2019). The residuals generated by the linear mixed models were visually checked to ensure the models were approximated to normal distribution by using the package 'ggResidpanel' and 'ggplot2' (Wickham, 2016). The package 'lme4' (Bates et al., 2015) was used for fitting linear mixed models with 'lmerTest' to evaluate significance (Kuznetsova et al., 2017).

Results

We had 92 observations from 55 individuals for vigilance behaviour. One individual fled mid-way through the focal at 21.6 s, so AD was recorded the same as FID. Additionally, two animals fled soon after the vigilance observation finished and before our subsequent approach explaining our two fewer FID estimates than focal estimates.

No significant variation in total vigilance was explained by treatment (Estimate = ±0.003, $P = 0.398$; Table 1), time interval (Estimate = 0.062, $P = 1.00$; Table 1) or the interaction between treatment and time interval (Table 1). Therefore, marmots did not change the proportion of time they allocated to total vigilance in response to experimental treatments and over time. Marmots were more vigilant when alert distance was greater (Estimate = 0.233, $P < 0.001$; Table 1), and females were more vigilant than males (Estimate = ±0.037, $P = 0.01$; Table 1; Fig. 1). However, marmots looked more towards observer holding a camera compared to when they were not holding a camera (Estimate = ±0.053, $P < 0.001$; Table 2). Marmots looked more towards observers when they first alerted at a greater distance (Estimate = 0.101, $P = 0.042$), and yearlings looked more towards observer than adults (Estimate = ±0.101, $P = 0.006$; Table 2; Fig. 1). Conversely, marmots allocated more time to looking away when the person approached them without a camera (Estimate = ±0.051, $P < 0.001$; Table 3). Here too, marmots spent more time to looking away from observer when they first alerted to the person at a greater distance (Estimate = 0.130, $P = 0.034$; Table 3), females looked away more than males (Estimate = ±0.038, $P = 0.044$; Table 3), and yearlings spent more time to looking away than adults (Estimate = ±0.037, $P = 0.042$; Table 3; Fig. 1). The time interval did not explain significant variation in the proportion of time allocated to looking towards observer (Estimate = 0.010, $P = 0.809$; Table 2) and looking away from observer (Estimate = 0.052, $P = 0.997$; Table 3).

Table 1 Results of a permutation test of the proportion of time allocated to total vigilance across four time intervals (0–15 s, 15–30 s, 30–45 s and 45–60 s) in yellow-bellied marmots

Variable	Estimate	*P*-value
Mu	0.359	1
Time interval	0.062	1
Alert distance	**0.233**	**<0.001**
Treatment: camera	0.003	0.398
Treatment: non-camera	−0.003	0.398
Sex: female	**0.037**	**0.01**
Sex: male	**−0.037**	**0.01**
Age_class: adult	−0.008	0.284
Age_class: yearling	0.008	0.284
Treatment:time interval (C:1)	0.130	0.94
Treatment:time interval (C:2)	0.016	0.914
Treatment:time interval (C:3)	−0.039	0.757
Treatment:time interval (C:4)	−0.103	0.992
Treatment:time interval (N:1)	0.155	0.812
Treatment:time interval (N:2)	0.030	0.826
Treatment:time interval (N:3)	−0.071	0.387
Treatment:time interval (N:4)	−0.117	0.986

Estimates of categorical variables are reported for each category. Statistically significant variables are shown in bold.

No significant variation in FID was explained either by the main effect of treatment (Estimate = 0.094, $P = 0.695$; Table 4) or by the interaction between treatment and AD (Estimate = −0.007, $P = 0.694$; Table 4). However, significant variation was explained by AD meaning that marmots flushed at greater distances when alerted at greater distances (Estimate = 0.886, $P < 0.001$; Table 4). While the yearlings flushed at greater distances than adults (Estimate = 0.153, $P = 0.029$; Table 4; Fig. 2), the interaction between experimental treatment and age class was not significant (Estimate = −0.069, $P = 0.425$).

Discussion

We tested whether the sight of a camera being pointed at an individual marmot influenced its vigilance and risk assessment. Together, our results show that marmots increased their vigilance towards humans when a camera was pointed at them, but that this experience did not impact the total proportion of time allocated to vigilance or the distance at which they fled following this experience. Thus, marmots paid attention to the camera but the experience of having a camera pointed at them does not seemingly modify their total vigilance or risk assessment. As far as we know, very few studies have experimentally evaluated the visual effect of cameras on wildlife, although nature photography has become a hugely popular type of human-wildlife interaction.

In this study, marmots looked towards humans more and looked at their surroundings less when the observer held up a camera, versus when the camera was not pointed at them. Many previous studies have tested 'gaze aversion' in animals (e.g. Goumas et al., 2020), and prior studies showed that animals become more sensitive while they are directly looked at

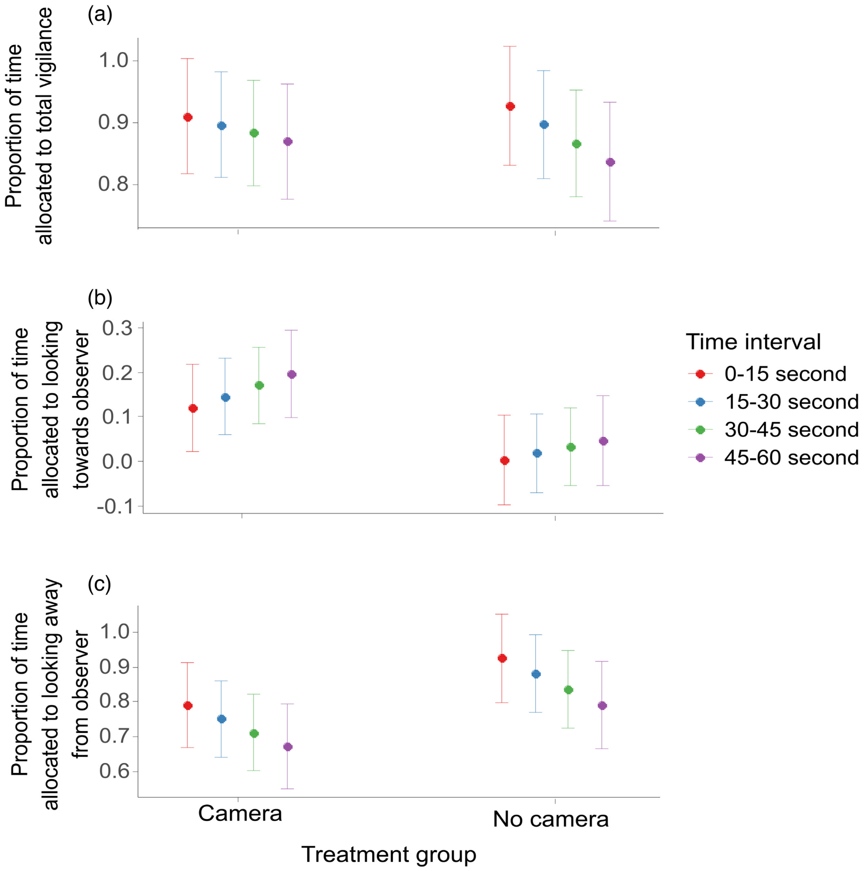

Figure 1 Marmots' responses to an approaching human with and without a camera. The *y*-axes represent (a) the proportion of time allocated to overall vigilance (the sum of (b and c)), (b) the proportion of time allocated to looking towards observer (when marmots' heads were pointed towards observers holding a camera) and (c) the proportion of time allocated to looking away from observer (when marmots' heads were pointed away from observers holding a camera). Means and standard errors show the behavioural responses in four different time intervals (0–15 s, 15–30 s, 30–45 s and 45–60 s).

and react more than when they are not looked at, suggesting that they perceived greater risk when humans look at them (Bateman & Fleming, 2014). In addition, many species have an innate fear of eyes, as seen in some butterflies and caterpillars that evolved eyespot patterns to reduce predation (Monteiro, 2015).

By capturing a marmots' attention, a person taking a photograph may reduce a marmots' ability to detect predators leading to a potentially fatal effect. Attention is a limited entity seen in many species (Chan et al., 2010), and animals cannot sustain high levels of vigilance for long periods of time (Dukas & Clark, 1995). Importantly, by reallocating their attention to the person with a camera, marmots were unable to scan for natural predators and this could have increased their vulnerability to predation. If predators avoid the areas that are actively visited by humans (the 'human shield' effect; Berger (2007)), the increased proportion of time to look at the human with a camera may not be serious. However, since predators (including canids and raptors) were present in our study area, decreasing the proportion of time allocated to looking around could increase predation risk. Whether capturing marmots' attention with a camera reduces predator detection abilities requires further study.

Although pointing a camera at a marmot increased the proportion of time allocated to looking towards humans, it is worth emphasizing that total vigilance during foraging was not modified. Therefore, we could not conclude that photography necessarily had an overall negative impact. Indeed, a prior study showed that marmots may habituate to humans if they are continuously exposed to them (Uchida & Blumstein, 2021). Since our field sampling was conducted in an area with considerable outdoor recreation (Morgan et al., 2021), marmots tended to tolerate some degree of human disturbance (Uchida & Blumstein, 2021). This habituation to humans might buffer potentially deleterious effects of photography, which might be an important behavioural strategy to cope with human disturbance. Although marmots may still need to monitor unusual human behaviours to assess the exposed risk, they may be able to sustain total vigilance levels by managing the proportion of time allocated to other behaviours. Such high behavioural

Table 2 Results of a permutation test of the proportion of time allocated to looking towards observer across four time intervals (0–15 s, 15–30 s, 30–45 s and 45–60 s)

Variable	Estimate	*P*-value
Mu	−0.037	**0.016**
Time interval	0.010	0.809
Alert distance	**0.101**	**0.042**
Treatment: camera	**0.053**	**<0.001**
Treatment: non-camera	**−0.053**	**<0.001**
Sex: female	−0.001	0.499
Sex: male	0.001	0.499
Age_class: adult	**−0.045**	**0.006**
Age_class: yearling	**0.045**	**0.006**
Treatment:time interval (C:1)	−0.016	0.102
Treatment:time interval (C:2)	0.030	0.298
Treatment:time interval (C:3)	−0.009	0.509
Treatment:time interval (C:4)	**0.048**	**0.016**
Treatment:time interval (N:1)	−0.009	0.138
Treatment:time interval (N:2)	−0.014	0.242
Treatment:time interval (N:3)	−0.049	0.182
Treatment:time interval (N:4)	0.019	0.094

Estimates of categorical variables are reported for each category. Statistically significant variables are shown in bold.

Table 3 Results of a permutation test of the proportion of time allocated to looking away from observer across four time intervals (0–15 s, 15–30 s, 30–45 s and 45–60 s)

Variable	Estimate	*P*-value
Mu	0.397	0.777
Time interval	0.052	0.997
Alert distance	**0.130**	**0.034**
Treatment: camera	**−0.051**	**0.001**
Treatment: non-camera	**0.051**	**0.001**
Sex: female	**0.038**	**0.044**
Sex: male	**−0.038**	**0.044**
Age_class: adult	**0.037**	**0.042**
Age_class: yearling	**−0.037**	**0.042**
Treatment:time interval (C:1)	0.147	0.563
Treatment:time interval (C:2)	−0.014	0.085
Treatment:time interval (C:3)	−0.031	0.675
Treatment:time interval (C:4)	−0.152	0.513
Treatment:time interval (N:1)	0.164	0.418
Treatment:time interval (N:2)	0.044	0.588
Treatment:time interval (N:3)	−0.021	0.704
Treatment:time interval (N:4)	−0.137	0.669

Estimates of categorical variables are reported for each category. Statistically significant variables are shown in bold.

flexibility is likely to be a key behavioural characteristic in highly disturbed environments (Sol et al., 2013; Uchida et al., 2019).

Animals may either habituate or sensitize if they are constantly exposed to non-threatening humans, which may also have fitness consequences. We divided the 60 s into four time intervals to test whether marmots decreased their behavioural responses over time as a function of the experimental treatments, meaning that they differentially habituated to the treatments. Although vigilance changed over 60 s, the experimental treatment did not result in significantly different responses over that time interval. Prior work has shown that marmots habituate to repeated experimental approaches (FID decreases over time: Runyan & Blumstein, 2004; Uchida & Blumstein, 2021) and such habituation to humans may increase vulnerability to predators (Geffroy et al., 2015). If animals habituate, and their fear response decreases due to cameras pointed at them, it may increase their vulnerability to real predators. Learning more about how animals change their vigilance response to repeated and long-term exposure to camera lenses may have important conservation implications.

We found that cameras captured yearling marmots' attention more than adults, indicating that the yearling marmots may be more sensitive to photography. This is similar to the result of a previous study which found that flight response to humans was more pronounced in juveniles than adults in herring gulls *Larus argentatus* (Goumas et al., 2020). Adult marmots may be less sensitive to the cameras because adults have already been repeatedly exposed to humans and therefore habituated to humans or humans with cameras. Alternatively, yearling marmots may be more attracted to a somewhat novel stimulus than adults. For example, in chimango caracaras (*Milvago chimango*), younger birds are more likely to explore novel objects and they are less neophobic than adults (Biondi et al., 2010). Since early-life learning experiences may have a significant effect on behaviours later in life (Hall et al., 2015), being exposed to cameras could have long-term effects on individuals. Additionally, since time allocation to vigilance is traded off with other important activities like foraging (Lima & Dill, 1990), increased vigilance may negatively influence the rate at which marmots gain mass. In yellow-bellied marmots, heavier individuals are more likely to survive hibernation (Cordes et al. 2020). Since we found that cameras captured yearling marmot's attention more so than that in adults, high levels of wildlife photography could conceivably negatively influence yearling over-winter hibernation survival by distracting them from foraging activity and preventing them from gaining sufficient fat reserves to survive winter.

Because our experimental treatment did not affect flight initiation distance or the interaction between alert distance and flight initiation distance, we can infer that wildlife photography may not influence subsequent marmot risk assessment. We caution that our FID results could reflect that when we resumed walking towards a subject, the camera was not focused on them. It is important to realize that vigilance and flight behaviours are two common antipredator responses often studied by behavioural ecologists. However, these behaviours are not necessarily tightly correlated. Although very few studies have rigorously tested the relationship between vigilance and FID, Uchida and Blumstein (2021) found that marmots had different patterns of vigilance while foraging and FID in response to long-term human disturbance. Therefore, animals may respond to human disturbance in various ways, and each response may reflect different underlying mechanisms of risk perceptions. Our results underscore the importance of focusing on multiple behaviours to study how animals may perceive and respond to humans.

Table 4 Results of a linear mixed effect model explaining variation in flight initiation distance (FID) in yellow-bellied marmots

	Estimate	SE	d.f.	*t*-value	*P*-value
(Intercept)	−0.28	0.18	88.33	−1.56	0.12
Experimental treatment: control	0.09	0.24	39.76	0.40	0.70
Alert distance (AD)	0.89	0.11	85.29	7.78	**<0.001**
Proportion of time looking towards observer	0.16	0.09	79.36	1.76	0.08
Sex: male	0.00	0.06	38.72	0.00	1.00
Age class: yearling	0.15	0.07	84.56	2.22	**0.03**
Experimental treatment: control * AD	−0.01	0.16	44.46	−0.05	0.96
Experimental treatment * age class: yearling	−0.07	0.09	34.03	−0.81	0.43
Random effects		Variance	SD		
Individual ID	(Intercept)	0.015	0.121		
Residual		0.03641	0.1908		

Statistically significant variables are shown in bold.

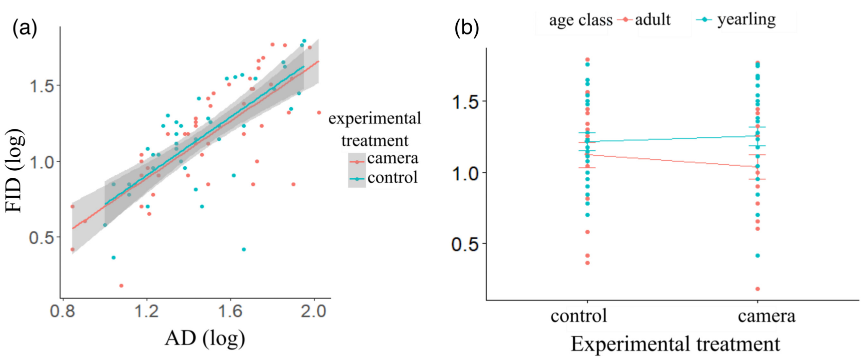

Figure 2 (a) The relationships between flight initiation distance (FID) (log10-transformed) and interaction between alert distance (AD) (log10-transformed) and experimental treatment group. Each line was calculated using the predicted probabilities from the linear mixed model. Buffers represent the 95% confidence intervals. While AD explained significant variation in FID, there was no effect of treatment on the relationship between AD and FID. (b) The relationship between FID (log10-transformed) and interaction between experimental treatment and age class. The interaction did not significantly explain variation in FID.

With more people venturing into areas with wildlife, it is important to identify anthropogenic impacts on wildlife to design proper mitigation. Although many studies indicate that human activity disturbs free-living animals (Chan et al., 2010; Fondren et al., 2019; French et al., 2011; Madsen & Fox, 1995; Meissner et al., 2015; Sibbald et al., 2011), a recent meta-analysis also revealed the neutral or positive effects of ecotourism on wildlife such as decreased flight behaviours and more time spent on fitness-enhancing activities (Bateman & Fleming, 2017). Since the responses of animals to human disturbance are complicated and often are not easy to interpret, focusing on several behavioural aspects is required to evaluate the effect of humans.

Our results may have insights into developing ecotourism protocols to minimize human impacts. Although wildlife photography may be a relatively low-impact activity as shown in the result that the total vigilance was not affected by camera presentation, this and previous studies (Huang et al., 2011; Slater et al., 2019) have also shown that it can distract antipredator behaviours and capture more attention, which potentially increases predation risk. Therefore, wildlife managers may consider regulating photography in locations where the predation risk might be particularly high or when vulnerable species ranges' overlap with human activities.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Model fitting strategy.