

# Conservation implications of habituation in Nubian ibex in response to ecotourism

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## Keywords

behavioral diversity; antipredator behavior; anthropogenic disturbance; flight initiation; habituation; vigilance; group size; Nubian ibex.

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## Abstract

Increased fragmentation and easier access to natural areas (e.g. ecotourism) is bringing man in closer contact to wild populations. Such encounters, even when they don't pose a direct threat to wildlife, may induce behavioral changes in animals that in the long run may have negative fitness consequences. We studied changes to the vigilance/group-size effect in Nubian ibex *Capra nubiana* in response to increased non-threatening anthropogenic disturbance in six sites, subject to different levels of ecotourism. In each site we regressed the average time ibex individuals devoted to vigilance on the size of the group they were with. We then compared the slopes and intercepts of the vigilance/group-size function between the six sites. We complimented these data with a study of how flight initiation distance (FID) changed between the six sites, as an indicator of the level of tolerance that ibex exhibit to increased anthropogenic presence. We found that as anthropogenic presence increased the vigilance/group-size function waned (i.e. the group-size effect was weaker). These findings were associated with reduced FID reflecting increased levels of tolerance, likely as a result of habituation in sites subject to high levels of ecotourism. The loss of the vigilance response as a function of group size may decrease the behavioral diversity in the ibex population. Wildlife habituation to increased non-threatening human activity alters key behavioral attributes that may ultimately impact social structure and other fitness-related characteristics.

## Introduction

Behavioral diversity is an important component in the resilience of individuals and populations (Berger-Tal & Saltz, 2016a; Cordero-Rivera, 2017). The ever-increasing anthropogenic footprint around the globe results in continually increasing contact between wildlife and anthropogenically-modified environments. Typically, such environments are characterized by reduced variance in many fitness-related attributes (e.g. productivity, risk of predation, refuge; McKinney, 2006). In salient species, this reduction in variance may reduce the expressed behavioral repertoire and eventually may result in the loss of heritable behavioral traits (Caro & Sherman, 2012).

With the worldwide increase in ecotourism and access of humans to natural areas, contact between wildlife and humans within natural habitats is frequent (Blumstein *et al.*, 2017). While this contact mostly constitutes a nuisance disturbance and usually does not pose any direct threat to the animals, such nuisance disturbances force animals, in many cases, to devote more time to safety-related behaviors, at the

expense of foraging activities (e.g. vigilance – Houston, McNamara & Hutchinson, 1993; Ruckstuhl, Festa-Bianchet & Jorgensen, 2003; Manor & Saltz, 2003; flight – Taylor & Knight, 2003; and avoidance or disturbed areas – Gander & Ingold, 1997). This trade-off between safety and obtaining resources ultimately affects population performance (McNamara & Houston, 1987) and social structure (Manor & Saltz, 2003), and highlights the importance of understanding the impact of human nuisance disturbance on the behavioral diversity of wildlife (McLean, 1997).

Occasionally, however, where human presence is common but harassment by humans is scarce, habituation may take place (Curio, 1993). Habituation is defined as a relatively persistent waning of a response, that results from repeated presentations of a stimulus not followed by any form of reinforcement and is not due to sensory or motor fatigue (Drickamer, Vessey & Meikle, 1996; Schakner & Blumstein, 2016), resulting in increased tolerance to the disturbance (Bejder *et al.*, 2009). Because habituation enables animals to devote more time to foraging and less to risk aversion, habituation responses have been considered superficially beneficial

in terms of conservation when the disturbance does not represent a real threat and is merely a nuisance (Fox & Madsen, 1997; Conomy *et al.*, 1998; Nisbet, 2000; Lord *et al.*, 2001; Gyuris, 2003). However, reduced risk aversion may pose a less obvious yet significant risk – namely, a shift in the selective forces towards favoring individuals that ignore potential risks by devoting less time to vigilance (Bejder *et al.*, 2009; Higham & Shelton, 2011; Geffroy *et al.*, 2015).

Antipredator vigilance is an important component in an animal's fitness, yet it is time consuming and, therefore, costly (Lima & Dill, 1990; Houston *et al.*, 1993; Illius & FitzGibbon, 1994). Consequently, animals are expected to optimize vigilance levels depending on the perceived threat in a given place and time (Beauchamp, 2008). Vigilance is one of the best examples of behavioral-modifications in response to threats. In ungulates, this behavior is typified by the animal interrupting its current feeding bout (or any other activity) and raising its head in order to detect any predators or other approaching hazards (McNamara & Houston, 1992; Bednekoff & Lima, 1998), but this comes at the cost of other fitness-related activities. In social species, belonging to a larger group is advantageous as the burden of vigilance can be shared (Jarman, 1974) and individuals investment in vigilance reduced. The reduction in individual vigilance as a function of group size (known as the vigilance/group-size effect – Lima, 1995), is one of the best-documented observations in the behavioral ecology of social animals (Hunter & Skinner, 1998; Beauchamp, 2015) and is considered a major evolutionary driving force of sociality in prey species. It is assumed to occur because of the lowered risk per individual in larger groups (dilution effect), and because each individual can rely also on the vigilance of other members in its group (many eyes effect) (Lima & Dill, 1990; Bednekoff & Ritter, 1994; Roberts, 1996; Lima & Bednekoff, 1999). Other factors may influence the vigilance/group-size effect: being part of a larger may increase intraspecific competition (so less time can be devoted to vigilance - Bednekoff & Lima, 2004) and increase predator attraction (so vigilance should increase - Roberts, 1996; Beecham & Farnsworth, 1999).

Theoretical models predict that increased human presence will impact the vigilance/groups-size function by elevating levels of vigilance to the maximum possible so the function becomes leveled towards the top; Paveri-Fontana & Focardi, 1994) and a field study (Manor & Saltz, 2003) corroborated this prediction. However, we know of no studies that looked at changes in the vigilance/group-size function in populations that habituate to anthropogenic presence.

Animals respond to disturbances (noise, movement, etc.) by becoming alert in order to assess the potential threat and respond appropriately. Typically, anthropogenic presence is viewed by animals as a threat (Benitez-Lopez, 2018). Occasionally, however, wildlife may learn that humans do not present a real threat (Higham & Shelton, 2011). Nevertheless, the initial audio, visual or olfactory sensing of anthropogenic presence requires some initial attention in order to determine that this initial stimulus does not reflect a real threat. We make a distinction between disturbances that are indicative of a threat and those that are no more than a

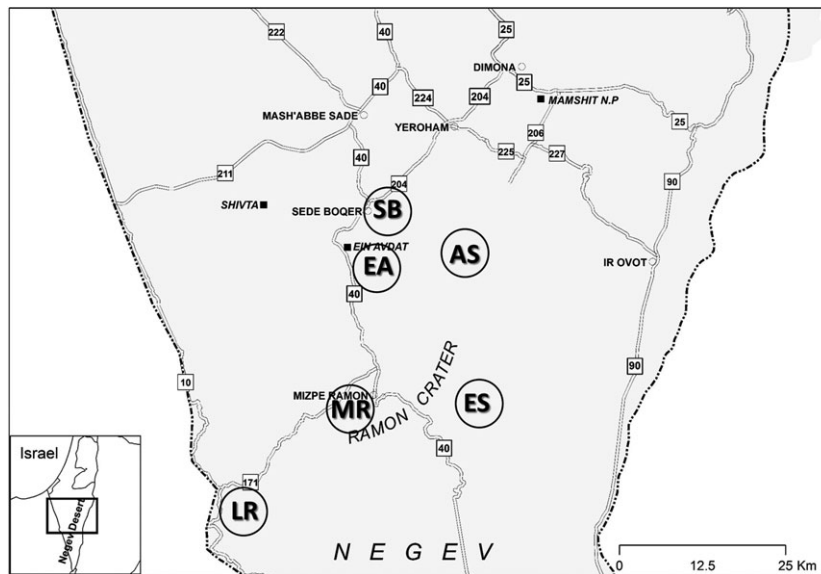
nuisance because they require some attention in order to determine that they do not reflect a true threat. The latter we term nuisance disturbances. As the frequency of nuisance disturbances (i.e. do not reflect a real threat) increases, the cost to fitness of responding to them increases. The cost per event of ignoring these signals (the probability of making a mistake and ignoring a real threat) is fixed. Thus, we hypothesize that as nuisance disturbance increases, the rate of response to disturbances (as a whole) should decrease and the vigilance/group-size effect should be dampened.

Here we test this hypothesis in a species known to habituate to human presence. The study focused on Nubian ibex *Capra nubiana* – a social desert ungulate that is listed as Vulnerable by the IUCN, and is typically found on or nearby cliffs in the vicinity of desert oases that are also attractive to tourists and hikers. Specifically, we studied changes in the vigilance/group-size function which we define here as a logarithmic decline of vigilance with group size between areas with varying intensity of tourism. We hypothesized that in ibex populations that experience heavy tourist traffic, habituation and the resulting increased tolerance will be accompanied by the flattening out of the vigilance/group-size function towards the lower vigilance values (as opposed to Manor & Saltz, 2003 where it flattens out towards the higher levels of vigilance). Thus, as tourist presence increases, the parameters of the regression of vigilance on group size will change – the intercept will decline and the regression coefficient will become less negative.

## Materials and methods

### Study area

The study was carried out between December 1999 and July 2001 in the Negev highlands region of southern Israel. The area supports several distinct ibex populations centered on oases (Shkedy & Saltz, 2000). No hunting (legal or otherwise) has been reported in the study area, but the ibex are exposed to human tourist activity in the form of hikers, bussed-tourism and off-road vehicles. The number of tourists varies considerably over time and space. We initially selected five study sites preferred by ibex and with varying intensities of human presence (Fig. 1): (1) Mitzpe Ramon (MR) township (UTM 6727.3883), located on the northern rim of the Ramon erosional cirque and subject to high levels of tourism. (2) Sde Boqer (SB) campus area (UTM 6703.4146) bordering the northern cliffs of the Zin riverbed and subject to high levels of tourism. (3) En Avdat (EA) National Park (UTM 6687.4118) with a high level of tourism that is restricted to daytime hours. (4) En Saharonim (ES) spring (UTM 6856.3873) located along the southeastern rim of the Ramon cirque, accessible to all vehicles, but relatively remote. (5) Aqev Spring (AS) area, (UTM 6734.4105) – a tributary of the Zin riverbed and accessible only by off-road vehicles or by foot. A sixth site, Lotz riverbed (LR) (UTM 6566.3744), a remote area with a very low level of human pressure, was added in December 2000. The sites are spread over a 1600 km<sup>2</sup> area with a distance of 5–40 km



**Figure 1** The six study sites in the Negev desert highlands: Mitzpe Ramon (MR) township; Sde Boqer (SB) campus area; En Avdat (EA) National Park; En Saharonim spring (ES); Aqev spring (AS); Lotz riverbed (LR).

between them. Each site is known to have a local population of ibex; as part of a different study we radio collared individuals in the first 4 sites and found little movement if any between the different sites including SB and EA that are only 5 km apart.

### Habituation and tolerance to human presence

We indexed the level of human presence in each site as the number of vehicles on site (or in most cases, at the parking lot at the entrance to the site) prior to the behavioral observations. To estimate the intensity of anthropogenic presence each car was considered four people while a bus was considered 40. In all sites the number of people arriving by foot is negligible. Because our study focused specifically on changes in the vigilance/group-size function in response to typical anthropogenic presence, our approach was parsimonious and we designed the study a-priori to minimize other sources of variance: (1) We collected data on weekdays during non-holiday periods which constitute the majority of time (~90%) and represent the common conditions the animals are exposed to, rather than the rare and acute events of holiday extremes (peak holidays are Passover, Hanukah, and Sukkoth which together account for 5 weeks of the year). (2) We excluded the rutting season. (3) We focused on females groups with young and observed adult female behavior. We calculated the mean  $\pm$  SE daily number of visitors in each site separately for the time periods just specified.

We assessed the level of tolerance using flight behavior (Stankowich, 2008). This was carried out after estimating the

number of visitors on the day of observation, followed by locating a group of animals, slowly approaching it and visually estimating the Flight Initiation Distance (FID – Blumstein, 2016), which is the distance to the closest individual at the point which the group begins moving away from the observer. Reduced FID is a measure of tolerance that may be the result of factors other than habituation (e.g. hunger or proximity to refuge). However, in this study all sites were typical ibex habitat consisting of a cliffy terrain and a nearby oasis, and the sites with more tourists are richer in resources, as well as more predictable in terms of resources. Thus, increased tolerance in such sites would most probably stem from habituation.

We then tested whether FID was affected by group size, and after removing the group-size effect (if necessary) calculated the mean flight distance in each of the sites. We used a Type III linear regression of the mean FID (to avoid pseudo-replication) on the index of human presence, weighting each point according to sample size.

### Vigilance/group-size relationships

Male ibex, twice the size of females, are less vulnerable to predation, allowing them to take greater foraging risks, whereas females and juveniles are more sensitive to predation and remain closer to the refuge provided by cliffs (Kohlmann, Müller & Alkon, 1996). These factors cause ibex to segregate by gender for most of the year in small herds of adult males and larger herds of females and juveniles (Gross, Alkon & Demment, 1995). Males and females unite only during the mating season (mid-September through mid-October).

We carried out our study during the non-mating season, focusing on groups of female-and-young. We observed ibex groups during daylight hours. Individual animal behaviors were recorded using scan sampling (Altmann, 1974). When a group was located, it was monitored for a maximum of 40 min. During this time, scans were carried out every 2 min with the aid of an 8 × 15 binocular or 15–45 × spotting scope (depending on distance to group). The two-minute frequency enabled the observers to improve their position in response to the animals' movement with little disturbance to the animals. We preferred scan sampling because we were not interested in rare occurrences, but rather the proportion of time devoted to vigilance. The same group and site were sampled only once on a specific day.

After a group was located and the group noticed the observer, the observer waited until all members of the group stopped looking in his direction and returned to normal activity. During this time group size and composition (sex and age – adults > 2 years, subadult, and juvenile < 6 month.) were recorded. In each scan the following behaviors were recorded: walking, running, feeding, resting (bedded), sleeping (bedded with eyes closed), vigilant while standing or resting. An ibex was considered vigilant if standing or bedded with the head above shoulder level observing the surroundings and not chewing (FitzGibbon, 1990). Visual attention to a specific disturbance was not considered as vigilance.

Each observation session provided a single data point for the regression of vigilance on group size. We calculated group size as the number of adults and sub-adults and calculated the % vigilance in the group as the total number of individuals observed vigilant in all scans divided by the sum of individuals observed in all scans. We then regressed vigilance on group size for each site separately. The relationship between vigilance and group size is not linear – as group size tends to infinity, vigilance is theoretically expected to go to zero (Motro & Cohen, 1989). Thus, for each of the six study sites, we used logarithmic regression  $y = \alpha + \beta \times \ln(x)$ ,  $x \geq 1$ , where  $x$  = group size, and  $y$  = vigilance measure,  $\alpha$  is the expected vigilance for a group of size  $x = 1$  (i.e., for a single-individual group), and  $\beta$  (the

slope) is the expected decrease in the vigilance measure if the logarithm of group size increases by 1. We can also consider  $\tau = \exp(\frac{-\alpha}{\beta})$  the group size for which the vigilance measure attains half its value for a single-individual group. Each of the three estimated parameters ( $\alpha$ ,  $\beta$  and  $\tau$ ) can be viewed as a function of the rate of disturbance, and a weighted linear regression was performed for each of these three functions. Note that by using only a single value of  $\alpha$ ,  $\beta$  and  $\tau$  for each of the six study sites, we avoided any problems associated with pseudo-replications, which result from repeated observation on the same individuals within each site. Data points in these analyses were weighted according to the number of observations in study site. In light of our working hypothesis,  $p$  values are given for a one-tailed alternative.

## Results

### Human presence and habituation

We estimated the number of visitors in each of the six sites based on 152 counting events. The mean number of visitors per event varied considerably between the sites ranging from  $2.91 \pm 6.17$  (SD) in LR to  $125.77 \pm 92.83$  in MR (Table 1). Group size did not affect FID ( $R^2 \leq 0.0001$ ,  $P = 0.992$ ,  $n = 152$ ), however, the ibex average FID/site was negatively correlated to the mean number of visitors ( $R^2 = 0.74$ ,  $P = 0.028$ ,  $n = 6$ ; Fig. 2), supporting the notion that ibex in heavily visited sites are more tolerant of humans.

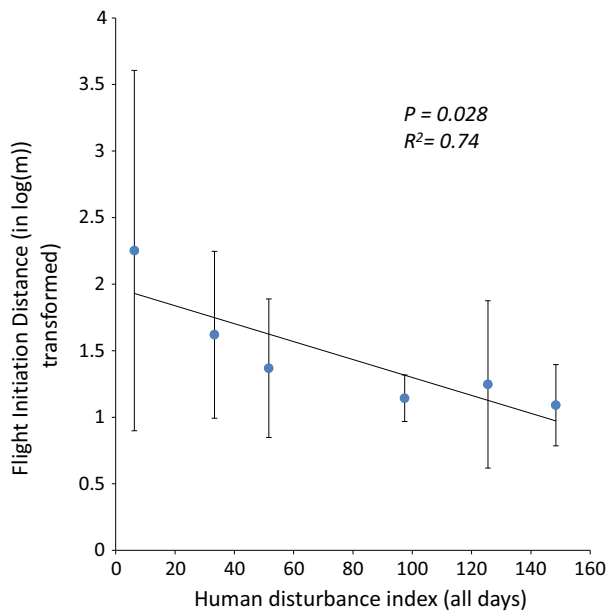
### Vigilance/group-size relationships

We observed ibex in 750 individual group sessions (MR = 223, SB = 129, EA = 125, ES = 122, AS = 120, LR = 31) on 211 observation days (Appendix S1). Group sizes ranged from 1–33. The vigilance/group-size regression slopes were negative for all sites (Table 1) – i.e., vigilance decreased with group size across levels of human disturbance. The intercepts of the regression of the vigilance over group size ( $\alpha$ ) declined with human presence, the regression

**Table 1** The index of human presence in each of our ibex field sites and the associated parameters of a logarithmic regression of vigilance on group size.

Site	Disturbance $\pm$ SD	No. of Observations	$\alpha \pm$ SE	$\beta \pm$ SE	$\tau$	$R$
Mitzpe Ramon (MR)	125.77 $\pm$ 92.83	223	0.415 $\pm$ 0.037	–0.033 $\pm$ 0.015	581.349	0.140
Ein Avdat (EA)	91.82 $\pm$ 80.17	125	0.350 $\pm$ 0.038	–0.033 $\pm$ 0.020	206.346	0.144
Sde Boker (SB)	72.52 $\pm$ 84.31	129	0.518 $\pm$ 0.049	–0.081 $\pm$ 0.027	24.566	0.329
Ein Saharonim (ES)	36.41 $\pm$ 48.88	122	0.529 $\pm$ 0.036	–0.075 $\pm$ 0.020	34.334	0.318
Aqev Spring (AS)	18.93 $\pm$ 23.02	120	0.529 $\pm$ 0.048	–0.082 $\pm$ 0.027	25.515	0.267
Lotz Riverbed (LR)	2.91 $\pm$ 6.17	31	0.693 $\pm$ 0.074	–0.107 $\pm$ 0.027	25.643	0.591

Human presence was calculated as the mean number of vehicles  $\pm$  1 standard deviation on site on non-holiday, non-rut periods, multiplied by their typical passenger capacity. The regression model was  $y = \alpha + \beta \times \ln(x)$ ,  $x \geq 1$ , where  $x$  = group size, and  $y$  = vigilance measure.  $\alpha$  is the expected vigilance for a group of size  $x = 1$  (i.e., for a single-individual group).  $\beta$  (the slope) is the expected decrease in the vigilance measure if the logarithm of group size increases by 1. We can also list  $\tau = \exp(\frac{-\alpha}{\beta})$ , the group size for which the vigilance measure attains half its value for a single-individual group.



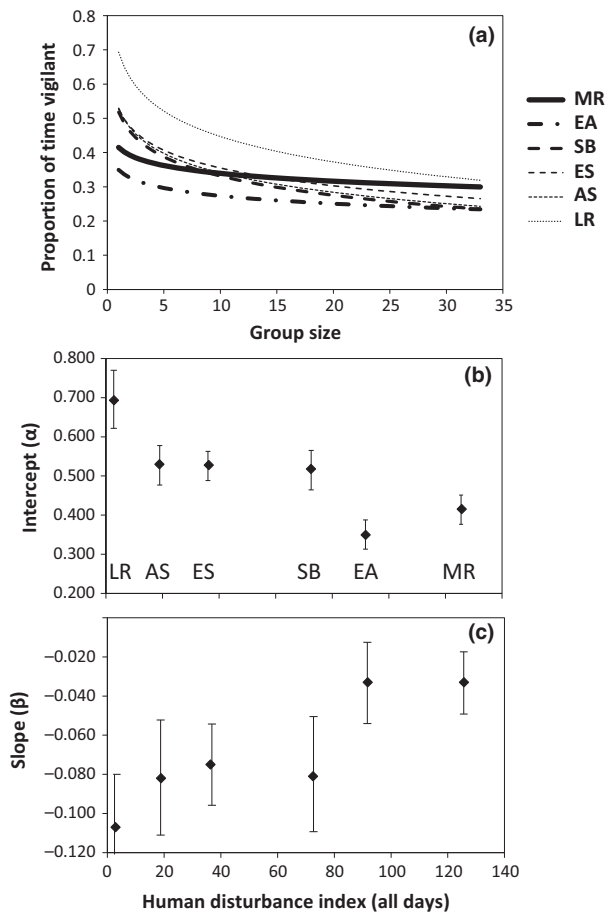
**Figure 2** The effects of the level of human disturbance on the flight initiation distance (FID) of Nubian ibex. FID is log-transformed and is given in meters. Error bars represent 1 standard error. Lower FID reflects increased tolerance to human presence, which in this study is the result of habituation.

coefficient ( $\beta$ ) became less steep, and the group size for which the vigilance measure attains half its value for a single-individual group ( $\tau$ ) increased (Fig. 3: Pearson's  $r$  and  $P$ -value =  $-0.7866$ ,  $0.0317$ ;  $0.8821$ ,  $0.0100$ ;  $0.8813$ ,  $0.0102$  for the three parameters, respectively). We found no effect of seasonality on the regression slopes ( $P > 0.2$ ).

## Discussion

Typically, disturbance by humans is expected to increase anti-predator behavior in prey species (Paveri-Fontana & Focardi, 1994). Because there must be an upper limit to the proportion of time that can be devoted to vigilance, increased disturbance is expected to flatten the vigilance/group-size curve towards the top, and some of the benefit provided by associating with a larger group will be lost (Manor & Saltz, 2003). However, in areas where human presence is common but harassment by humans is scarce, habituation may occur.

Our findings regarding FID reflect increased levels of tolerance to humans with increased human presence. There is no evidence to suggest that the observed increased levels of tolerance are the result of adverse conditions experienced by the ibex (e.g. hunger) – the abundance of natural resources for ibex in all study sites is roughly the same and probably even higher around oases where human presence is elevated (we note here that it is illegal to feed the ibex). We therefore conclude that the observed tolerance is probably the outcome of habituation. Two factors may contribute to this habituation: (1) the cost of the frequent responses to the recurrent



**Figure 3** The effect of the intensity of human disturbance on the vigilance/group-size function in Nubian ibex: (a) The slopes for the six different sites with varying levels of human nuisance disturbance (thicker lines reflect more disturbance); (b) The y-intercept at the point where group size = 1, of the vigilance/group-size curves in relation of human nuisance disturbance; (c) The regression coefficient in relation to disturbance. The index of human nuisance disturbance was measured as the number of vehicles on site at the time of the behavioral observations multiplied by their capacity ( $\sim$ number of car seats).

nuisance disturbances that pose no real threat may exceed the perceived cost associated with risk of predation, and (2) the increased anthropogenic presence that may be associated with decreased risk of predation (Leighton, Horrocks & Kramer, 2010; Shannon *et al.*, 2014). Increased anthropogenic presence, however, may also result in increased predator densities and elevated risk of predation (Bino *et al.*, 2010; Rodewald, Kearns & Shustack, 2011). For ibex, where group association is not fixed, an increase in predation risk with increased human presence is expected to cause a decrease in vigilance in larger groups and an increase in smaller groups (Bednekoff & Lima, 2004), making the slope of vigilance/group-size steeper (more negative). This did not occur in our study and was not expected since the only predator in this region is the Indian wolf *Canis lupus pallipes* that occurs at

low densities and does not appear to be more common around heavily touristed areas.

Thus, as nuisance disturbance increases the perceived cost of vigilant behavior exceeds its benefits and should be reduced to a minimum. Yet, although vigilance rates in our study were reduced with increased anthropogenic presence, they remained well above zero, even in the larger groups. This suggests the existence of a non-zero threshold. If a single vigilant individual is sufficient for the entire herd, then simple theoretical considerations predict that an individual's vigilance should tend to zero as herd size increases. In reality, however, this does not occur, for several reasons: (1) Coordination among herd members, if exists, tends to diminish as herd size increases, leading to overlapping in vigilance performance. (2) The cost of vigilance, reflected by the time not devoted to eating (or other activities), is smaller if the probability of vigilance is small, due to the diminishing returns associated with feeding. (3) Large herds are more conspicuous to predators, thus requiring a greater amount of vigilance. (4) The greater dispersion of large herds requires more than a single observer for covering the entire area. Hence, it is not surprising to find that actual vigilance does not fall below a positive threshold and the reduction in vigilance is more pronounced in the smaller groups.

Nevertheless, our results show that the vigilance/group-size function of the ibex becomes flattened out towards the bottom as anthropogenic nuisance disturbance increases, and a key advantage of associating with conspecific is lost. Interestingly, when disturbance frequency increases and no habituation takes place, vigilance is maximized regardless of group size (e.g. Manor & Saltz, 2003) and the vigilance/group-size function is also flattened, albeit towards an upper threshold. This means that although the functional response to increased levels of disturbance differs completely depending on whether the disturbance is merely a nuisance and individuals respond to the disturbance by habituation and reduction of vigilance, or whether the disturbance is real, and individuals respond by elevating their level of vigilance, the outcome is similar: the flattening of the vigilance/group-size function resulting in reduced benefits of being in a group because vigilance rates remain similar regardless of group size.

Anthropogenic-induced behavioral changes are commonly considered conservation concerns (Berger-Tal & Saltz, 2016b). Habituation is an exception and is often perceived as a positive response to anthropogenic disturbance (Batesman & Fleming, 2017). While this may be true over the short term, ultimately such behavioral changes reflect a substantial alteration in the selective forces operating on a population (Newsome *et al.*, 2017) and may result in the loss of behavioral diversity (Cordero-Rivera, 2017). One expression of this diversity is behavioral flexibility which is sustained by the gene by environment (G×E) interaction. Behavioral flexibility is an important component in the fitness of animals where much of this flexibility results from learning, including maternal effects. Changes in environmental conditions may, therefore, bring about the loss of this

flexibility by reducing the behavioral repertoire an animal possesses, thereby limiting the range of behaviors that can be expressed. Because maternal effects may play an important role in learning, loss of this flexibility within populations may take many generations to recover from and irreversible genetic changes may occur during this time (Littleford-Colquhoun *et al.*, 2017). Thus, in contrast to Batesman & Fleming (2017), we conclude that wildlife habituation may have severe negative impacts on populations in the form of lost behavioral diversity.

Our results address only the common day-to-day disturbance levels. Tadesse & Kotler (2012) have demonstrated, using a giving up density experiment, that deviations from the common visitor pressure may still elicit a response in the ibex, however, their study was restricted to only one of our six sites (EA) that is closed to visitors during the dark hours. Nevertheless, because tourism is not expected to diminish in the future, over time this response to peak visitor levels may wane as well.

## Conclusions

In the contemporary Anthropocene, increased fragmentation and accessibility to natural areas (e.g. ecotourism) is bringing man in closer contact to wild populations (Heywood, 1995). Often, this contact manifests a mere nuisance disturbance and does not constitute a direct threat to wildlife. However, such nuisance disturbances may induce animals to modify their behavior, becoming habituated and reducing their anti-predator behavior (Geffroy *et al.*, 2015). Such changes in behavioral patterns and life histories receive limited attention in conservation decision-making (Caro & Sherman, 2012). In fact, such changes are often considered harmless and even desirable (Bejder *et al.*, 2009), while in the long-run, may actually be mal-adaptive.

The vigilance/group-size function is an important component of social organization in social animals. Significant changes in this function signify changes in the evolutionary forces that drive the structure of social animal societies and are, in effect, a form of biodiversity loss (Cordero-Rivera, 2017). Any changes in this function, and especially its loss, induced by anthropogenic interference, may reflect a significant change in the evolutionary trajectory of the species, the consequences of which are difficult to predict (Ehrlich, 2001).

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## Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** Proportion of time vigilant as a function of group size of Nubian ibex (*Capra nubiana*) in six areas with varying levels of tourism (labeled as disturbance index). Lines represent logarithmic regression model (see Table 1 in main text)