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# Potential impact of trophy hunting on vigilance and flight behaviour in Blue Sheep (Bharal: *Pseudois nayaur*)

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ABSTRACT

Conservation management is often integrated into a broader tourism context, and under some conditions allows wildlife trophy hunting to support its goals. In such cases it is generally acknowledged that the direct impact of hunting requires careful monitoring and regulation with respect to the size and dynamics of hunted populations. However, hunting may also affect the behaviour of local wildlife, including their reaction to the approach of humans. Thus, hunting may have broader consequences on tourism and conservation management if animals respond by changing their behaviour in a way that makes them more difficult to monitor or for tourists to observe. We examined the potential impact of trophy hunting on vigilance and flight behaviour of Blue Sheep (Bharal: *Pseudois nayaur*) in Nepal, by comparing their behavioural responses in conservation areas with contrasting management approaches: the Dhorpatan Hunting Reserve (DHR) where male Blue Sheep have been trophy hunted since the 1980 s, and the Annapurna Conservation Area (ACA) where hunting is forbidden. Blue Sheep in the DHR had higher levels of vigilance than sheep in the ACA (10 % versus 8 % of their time respectively). Sheep in the DHR were also much more difficult to approach on foot, with Blue Sheep groups in the DHR having an average flight initiation distance of 96 ± 7 m versus 39 ± 3 m for the ACA, and subsequently moving much greater distances when disturbed (flight movement distance in the DHR versus ACA: 79 ± 3 m versus 26 ± 2 m respectively). These results suggest that hunting impacts on tourism and conservation may extend well beyond the population dynamic consequences of trophy animal removal. These behavioural effects suggest additional consideration is required when balancing wildlife hunting and observation tourism activities in the same area. It would also be valuable to assess the impacts of hunting-induced behaviour changes on the effectiveness of wildlife monitoring in such areas.

## 1. Introduction

Conservation planning often requires consideration of coexistence between human activities and the needs of wildlife populations (e.g. Johansson et al., 2016; Aronsson and Persson, 2017). Wildlife tourism is one aspect of such an approach, where the local economic benefits of tourism attaches additional value to wildlife to help promote their preservation (Sekhar, 2003). However, wildlife tourism takes many forms and it is important for conservation managers to understand how different tourism approaches may impact

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focal wildlife populations. One of these impacts relates to how human disturbance from tourism influences animal behaviour (Setsaas et al., 2018), and subsequently alters relationships between tourists, animals and conservation goals (Clemmons and Buchholz, 1997; Berger-Tal et al., 2011; Greggor et al., 2019). This can become a significant issue if the animals' behavioural response to human disturbance is at odds with the aims of tourism engagement (Buckley and Mossaz, 2015) or negatively affects population dynamics and persistence (Clemmons and Buchholz, 1997; Setsaas et al., 2018).

In Nepal, tourism engagement and conservation management of Blue Sheep (or Bharal: *Pseudois nayaur*) can be contrasted between a wildlife preservation approach employed in the Annapurna Conservation Area (ACA), and a trophy-hunting management focus employed in the Dhorpatan Hunting Reserve (DHR). The ACA is the largest protected area in Nepal and promotes the concept of ecotourism where tourist interactions with wildlife are based on viewing the animals in their natural habitat (DNPWC, 2012). In contrast, the DHR uses wildlife trophy hunting as a key component of its tourism management plan (Aryal et al., 2015; DHR, 2019; NTNC, 2022). Although hunting has been the main focus of wildlife tourism in the DHR since the 1980′s (Aryal et al., 2010, 2015), current management recommendations now include promoting other forms of ecotourism in this area (DHR, 2019). Both the ACA and DHR are similar in their habitat structure and wildlife diversity, and are part of the same conservation region in Nepal. Within this region Blue Sheep are a major keystone species (Aryal et al., 2014; Filla et al., 2021, 2022) and are the most frequently trophy-hunted animal (Aryal et al., 2015; DHR, 2019; NTNC, 2022). While both approaches to conservation have been successful at generating considerable revenue from tourism (DNPWC, 2012; DHR, 2019), it is likely that these different tourism activities (observation versus hunting) have different impacts on the behavioural profiles of focal wildlife species (Setsaas et al., 2007, 2018; Muposhi et al., 2016).

For a comprehensive assessment of the impact of trophy-hunting on target populations, such as Blue Sheep, it may be insufficient for conservation managers to limit their evaluation to the population demographic consequences of hunting (e.g. Karki and Thapa, 2013; Aryal et al., 2015; DHR, 2019; NTNC, 2022). Sustainable wildlife tourism also requires an understanding of the behavioural responses of the animals to human disturbance (Caro and Berger, 2019) from two perspectives. The first is related to the animals, where human-induced changes in the animals' movement (in space and time) or behavioural profiles (e.g. feeding, predator avoidance) may result in long-term consequences for the health and viability of individuals or populations (Setsaas et al., 2018). The second perspective relates to the tourism experience itself, with changes in animal behaviour potentially conflicting with tourist expectations, resulting in reduced satisfaction and long-term consequences for tourism development. An obvious example would be an increase in animal flight distances as a consequence of hunting (Stankowich, 2008; Muposhi et al., 2016), resulting in a reduced ability for tourists to approach and view (or hunt) these same animals. This suggests a clear role for including an animal behavioural perspective when assessing the effect of different approaches to wildlife tourism and conservation (Caro and Berger, 2019).

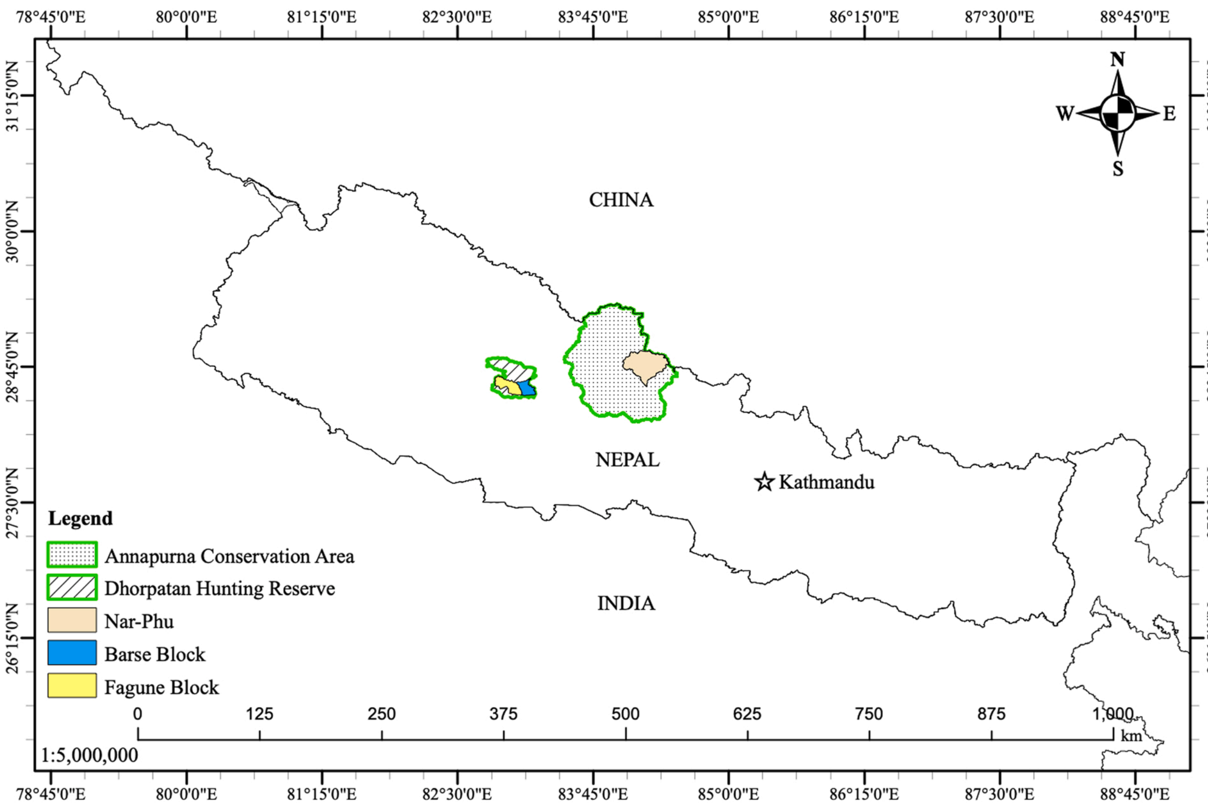


**Fig. 1.** Location of the study areas in Nepal: The Annapurna Conservation Area (dotted) with the Nar-Phu region shaded brown, and the Dhorpatan Hunting Reserve (shading lines) with the Barse and Fague Blocks, where the study was conducted, shaded blue and yellow respectively.

In this study we take advantage of the differences in conservation management between the ACA and DHR to evaluate the potential effect of trophy hunting on key behaviours in a target wildlife species. We specifically focus on comparing vigilance and flight behaviour of Blue Sheep in the two reserves. These behaviours were primarily selected because of their relationship with how the animals interact with wildlife tourists, in addition to their potential link to individual fitness. Vigilance behaviour, where an animal spends time and energy surveying an area for a potential predator, may come at the expense of restorative behaviours such as foraging or reproduction (Houston et al., 1993; Muposhi et al., 2013; Setsaas et al., 2018). Flight behaviour, where animals move away at the approach of humans, is not only disruptive to the animals, but also threatens to change the wildlife tourism experience if these animals increasingly avoid humans and do not show their natural behaviours when people are nearby. Here we expect that trophy hunting in the DHR would result in increased flight responses and vigilance behaviour compared to groups in the ACA (Caro, 2005; Stankowich, 2008; Setsaas et al., 2007, 2018; Muposhi et al., 2016). We use focal animal behavioural sampling and a simple flight distance response test to compare the behaviour of Blue Sheep in these two areas.

## 2. Methods

### 2.1. Study areas

The study was conducted in Dhorpatan Hunting Reserve (DHR) and Annapurna Conservation Area (ACA), in northern Nepal (Fig. 1) during the 2021 autumn hunting season. These two protected areas are representative of the high-altitude ecosystem that blue sheep inhabit, but each area falls under a different management authority. DHR is managed by the Department of National Parks and Wildlife Conservation, and is the only place where sport hunting of blue sheep is allowed in Nepal. The ACA is managed through a long-term participatory integrated conservation and development program run by a non-governmental organization, the National Trust for Nature Conservation. Within the ACA only non-lethal human recreational activities such as photographic ecotourism are permitted, while the major source of revenue in the DHR is trophy hunting (DHR, 2019).

The DHR (28°15’ N to 28°55’ N and 82°25’ E to 83°35’ E) covers an area of 1325 $km^2$ and is between 2000 and 7246 m a.s.l. It is covered by forest at lower elevations and grasslands at elevations above the tree line (Kandel et al., 2011; DHR, 2019). The alpine pastures above 4000 m, locally known as Patans, are important habitats for herbivorous animals like Blue Sheep. Hunting within the DHR is administered across seven areas: it is in two of these areas (the Fagune and Barse blocks covering 494 $km^2$), that the study is located (Fig. 1). These two hunting blocks within the reserve have the highest hunting pressure because they are the most easily accessible (DHR, 2019); consequently they also face the highest prevalence of Blue Sheep poaching in the reserve (NTNC, 2022). Trophy hunting is authorized twice a year, in the spring (March–April) and the autumn (October–November), and the number of trophy males that may be hunted is regulated by the Department of National Parks and Wildlife Conservation to an annual quota of between 25 and 32 individuals; although in most years this quota is not reached (DHR, 2019; NTNC, 2022).

Within the ACA our study is located in the Nar-Phu region (28°40′–28°50′N, 84°5′–84°13′E, Fig. 1), a community-designated protected area providing high quality habitat for Blue Sheep and other herbivores. The Nar-Phu region (473 $km^2$), often known as "The Little Tibet," is one of the pristine and untouched regions in the Annapurna Conservation Area. The area was only made accessible to tourists after 2002, and entry into this area requires a specific permit. There are less than 600 persons living in this area, making it among Nepal’s least populated area. Tibetan ethnic communities in this region follow native Buddhist traditions that have not been influenced by the outside world and view the killing of any living creature as a sinful action; here, there are no records of illegal hunting of Blue Sheep. Before field visits to both sites, all potential habitat areas as characterized by frequent blue sheep sightings, and known alpine grassland habitats were identified through staff interviews and consultation with local herders.

### 2.2. Behavioural surveys

Surveys were conducted in Oct-Nov 2021, during the autumn hunting season, by two teams that included an observer and an experienced local field assistant, during morning (6:00–11:00) and afternoon hours (14:00–17:00) when sheep activity is high (Liu et al., 2005). Study sites were divided into sub-blocks based on natural geographic barriers (e.g. ridges and rivers) to minimise the possibility of groups being double counted; this risk was further minimised by sampling blocks sequentially. Within each area, an existing trail that coincided with the movement patterns of sheep was used. Blue sheep are more likely to be found in the valleys in the early morning for accessing water and then progressively ascend while foraging, to reach relatively secure areas on ridge tops by dusk where they rest for the night (Schaller, 1973); thus, trails were used that allowed us to search for sheep across all elevations. Observations were made using vantage points 200–250 m distance from groups using a spotting scope (20 × 80) or binoculars (10 × 42). Whenever a group was encountered, the observer recored individual sheep behaviour using the scope, while the field assistant recorded group and terrain details (i.e. date, GPS coordinates, group size, sex, and age classes). Unique features of individuals, such as broken horns and coloration patterns were also noted, to distinguish the different herds. Local habitat parameters were also recorded and related to individual group observations (distance to escape cover, human settlements and trails). Solid rocky cliffs with inclinations greater than 75 degrees, resting on narrow ledges were considered escape cover (Wilson, 1981); Blue Sheep can ascend these extraordinarily steep slopes to seek sanctuary when they are threatened by predators such as the snow leopard.

#### 2.2.1. Vigilance behaviour

We undertook focal behavioural observations on 235 individual sheep (136 from DHR and 99 from ACA) comprising 2392 min of observation time (1382 mins DHR; 1010 mins ACA). For these observations the observer located an individual using the scope or binoculars and then started a stopwatch to record the total time spent observing each individual (focal animal sampling), with the aim to follow each individual for 10 min (range of observations was 524–626 s for n = 235 individual sheep). During an observation, the duration of different behaviours were continuously recorded so that the proportion of time spent of each behaviour could be determined (using the software EthoLog 2.2.4; Ottoni, 2000). Behaviour was recorded as four mutually exclusive behavioural types: foraging (grazing, browsing and ruminating), walking (moving for a minimum of four consecutive steps), vigilance (head high, ears forward and not moving, eyes staring), or 'other' (which included resting, grooming and sexual behaviour). Other behaviours were recorded to assess which behaviours may be 'traded-off' for increased vigilance. Behavioural data were not collected until all sheep in the group ignored our presence if we were detected, which usually took less than 10 min, to minimise any influence of observer presence (Kiffner et al., 2014). When the focal sheep was no longer visible or after a 10-minute observation period, the focus was shifted to another individual of the same flock. In a small number of cases, multiple sheep could be observed simultaneously and their behaviour recorded. Only nursery herds (i.e. herds with adult males, females and juveniles/lambs; the most common herd structure (Wegge, 1979)) were observed, and within these the behaviour of adults and yearlings were recorded.

#### 2.2.2. Flight initiation distance and flight movement distance

Flight initiation distance is the distance at which an animal responds to the approach of a person by moving or running away (i.e. how close a person can approach the group without it moving). The distance the group subsequently moves before stopping and resuming normal feeding or grooming behaviours is the flight movement distance. These behaviours are a simple and standardised measure of tolerance to different levels of threats in disturbance studies (Weston et al., 2012; Barros et al., 2016). Both behaviours are expected to be related to each other, with animals showing both an increased flight initiation and movement distance when it perceives the threat to be higher (Brown et al., 2012). These measures were undertaken after all other behavioural measures had been recored for the group (see above), using the method described by Setsaas et al. (2007). For this, one person walked towards the group at a constant speed of 0.5 m per second, and continuously measured the distance between themselves and the centre of the group using a laser rangefinder (Astra Optix OTX1600: accurate to within 1 m). This was used to determine the 'flight initiation distance' (see also Holmern et al., 2016), as the distance between observer and group at the moment the sheep turned and began to moved away from the approaching person. When the group stopped, the distance they had travelled during this movement was also recorded, as their 'flight movement distance'.

### 2.3. Data analyses

For summarising behavioural differences between sheep in the different sites (DHR versus ACA), we used generalized linear modelling implemented in R (R Core Team, 2022). For the flight distance analyses based at the group level, we used a GLM framework with a gamma likelihood distribution because the distance data were > 0 and positively skewed. For these we used an identity-link function meaning that all regression coefficients remained in the same scale as the response variable. We mean centred explanatory variables so that the intercept had a direct biological interpretation (i.e. the mean flight distance response for animals in the ACA area, with the site parameter detailing the difference in the flight distance of animals in the DHR area). For the individual-level analysis examining vigilance, we used a mixed-model beta-regression GLMM implemented in the package 'glmmTMB' (Brooks et al., 2017). A beta likelihood distribution was used because vigilance was analysed as the proportion of total time observed (i.e. time vigilance / time observation for each individual animal); thus all regression coefficients for the vigilance analyses are presented at the logit scale. A random effect based on the social group that individuals belonged to was included to control for potential group-level effects in behaviour related these social clusters. In addition to the effect of site (DHR vs ACA), we also considered other explanatory variables primarily to ensure that differences between groups and sites did not confound our estimates of between-site differences. These variables include the distance to the nearest human settlement, the distance to the nearest human trail, distance to cover, group size and the proportion of males in the group. Because we estimated the effect of these other explanatory variables on the response variable,

**Table 1**
Parameter estimates from logit-link beta GLMM regression with their associated t-statistic and p-value showing the relationship between predicted vigilance of an individual Blue Sheep (as a proportion of their time budget), and individual-level variables (age [yearling vs adult], individual sex) and group-level variables (site, proportion of males in group, and distance measures). The site-level parameter is the difference between animals in the Dhorpatan Hunting Reserve (DHR) compared to those in the Annapurna Conservation Area (ACA; i.e. the intercept value). Note that all parameters are at the logit scale, and other explanatory variables were mean centred, so that the interpretation of the intercept is relative to explanatory variables being set at their mean value.

| Parameter | Estimate (mean ± SD) | t-statistic | p-value |
|---|---|---|---|
| Intercept (ACA) | -2.86 ± 0.12 | 23.1 | < 0.00001 |
| Site (DHR) | 0.252 ± 0.09 | 2.78 | 0.005 |
| Age | 0.41 ± 0.11 | 3.89 | < 0.0001 |
| Distance to settlement (m) | 0.0002 ± 0.0001 | 3.04 | 0.002 |
| Proportion males in group | 0.56 ± 0.22 | 2.51 | 0.011 |
| Individual sex | 0.089 ± 0.062 | 1.42 | 0.15 |
| Distance to trail (m) | 0.0001 ± 0.0002 | 0.78 | 0.43 |
| Group size | 0.002 ± 0.004 | 0.48 | 0.62 |
| Distance to cover (m) | 0.0001 ± 0.09 | 0.46 | 0.64 |

we also include these estimates (i.e. for both vigilance and flight distance) as an exploratory form of analysis that could inform future study. However, since the number of parameters being estimated in these models is relatively high compared to the amount of data collected, we suggest caution when interpreting the influence of these variables on flight distance and vigilance behaviours.

## 3. Results

### *3.1. Vigilance behaviour*

During observations, sheep spent approximately 65 % of their time feeding, 25 % of their time walking and 9 % of their time engaging in vigilance behaviour (Table S1). Based on the individual sheep observations across groups, there was clear evidence that vigilance behaviour was approximately 25 % higher in the hunting area compared to the protected area (proportion of time spent in vigilance behaviour in DHR vs ACA: 0.104 ± 0.006 vs 0.082 ± 0.004; Table 1). There was also evidence that vigilance behaviour was related to individual age, distance to nearest human settlement and the proportion of males in the group (Table 1). When comparing behavioural profiles of animals between DHR and ACA, it appeared that the increase in vigilance in the DHR was compensated for with reduced walking time (as the proportion of feeding time remained constant between the two sites; Table S1). We subsequently tested for an interaction effect between site and distance-to-settlement to determine whether habituation effects were more pronounced in protected versus hunting areas; however this was not significant (0.0003 ± 0.0008; $p = 0.69$). As a behavioural comparison, the proportion of time individuals spent feeding did not differ between sites; however, the time spent feeding was related to group size, distance to cover, individual age and the proportion of males in the group (Table S2). Interestingly, age and the proportion of males in the group had contrasting effects on vigilance (positive) and feeding behaviour (negative).

### *3.2. Flight initiation and movement distance*

Based on the raw observational data of group behaviour, the flight initiation distance was almost three times the distance for sheep in the hunting area (DHR mean ± SD; 106 ± 25 m) compared to the protected area (ACA; 39 ± 7.3 m; Table 2). For flight movement distance, there was an almost fourfold difference between sites (DHR vs ACA; 82 ± 19 m vs 21 ± 4.6 m). However, the data ranges for potential confounding explanatory variables influencing flight distance behaviours varied between these two areas (Table 2). Thus, we also modelled the effect of site (DHR vs ACA) conditional on the effect of these other variables in a multiple regression. These analyses showed that even when distance to human settlements, trails, cover and group size were accounted for, the effect of site was similarly large for both flight initiation and movement distances (predicted flight initiation distance was 96 ± 7 m versus 39 ± 3 m; predicted flight movement distance was 79 ± 3 m versus 26 ± 2 m for DHR vs ACA sites respectively, when other explanatory variables were set at their mean value observed within the ACA area; Table 3). This modelling also suggested that the distance of the group to the nearest human settlement or walking trail was positively related to both flight distance measures, and group size was related to flight movement distance (Table 3). There was little evidence in our data that the effect of distance to settlements and trails differed in their effect on FID and FMD between sites, based on the addition of interaction terms (Table S3). There was no evidence that distance to cover played a role in influencing flight distance behaviour.

## 4. Discussion

In this study we show that trophy hunting may have large effects on the behaviour of Blue Sheep, in addition to the reported potential for impacts on population dynamics (Wegge, 1979; Aryal et al., 2010, 2015; Karki and Thapa, 2013; DHR, 2019; NTNC, 2022). This was possible through comparisons between adjacent conservation areas with different management approaches, which demonstrated considerable increases in the vigilance and flight distance behaviours of Blue Sheep in the presence of hunting. Yet despite these patterns being largely consistent with other studies (e.g. Stankowich, 2008; Muposhi et al., 2016; Setsaas et al., 2018), we remind the reader that our conclusions need to be interpreted with some caution because of the necessary limitation of the design of the study: i.e. Nepal has only a single hunting reserve (i.e. DHR) where the effect of trophy hunting on wildlife can be measured. Although the DHR provides important research opportunities to compare the impact of trophy hunting to non-hunting conservation areas, it must be considered that some of these measured differences between sites may arise from unaccounted-for site-specific effects (e.g. higher illegal hunting activities in the DHR or local differences in predation pressure may be the reason for behavioural differences,

**Table 2**
Raw data ranges for group observations of Blue Sheep in the Annapurna Conservation Area (ACA) and the Dhorpatan Hunting Reserve (DHR).

| Observed parameter | ACA | DHR |
|---|---|---|
| Group size | 9–37 | 5–26 |
| Distance to cover (m) | 72–134 | 8–487 |
| Distance to settlement (m) | 226–410 | 127–2105 |
| Distance to trail (m) | 200–285 | 12–975 |
| Proportion of males | 0.41–0.57 | 0.14–1 |
| Flight Initiation Distance (m) | 29–47 | 84–176 |
| Flight Movement Distance (m) | 17–27 | 68–134 |

**Table 3**
Parameter estimates with their associated t-statistic and p-value from identity-link regressions showing the relationship between group-level parameters and Flight Initiation Distance (FID; top) and Flight Movement Distance (FMD; lower). In both regressions the predicted effect of site on the flight distance (in metres) can be determined for the Annapurna Conservation Area (ACA) from the intercept value, and for the Dhorpatan Hunting Reserve (DHR) from the addition of the intercept and the site parameter. All other explanatory variables were mean centred, so that the interpretation of the intercept is relative to explanatory variables being set at their mean value.

| Parameter | Estimate (mean ± SD) | t-statistic | p-value |
|---|---|---|---|
| Flight Initiation Distance | | | |
| intercept (ACA) | 39.6 ± 3.38 | 11.7 | < 0.0001 |
| site (DHR) | 56.5 ± 7.69 | 7.35 | < 0.0001 |
| distance to settlement | 0.016 ± 0.008 | 1.79 | 0.11 |
| distance to trail | 0.036 ± 0.021 | 1.66 | 0.13 |
| proportion males | 22.9 ± 20.7 | 1.10 | 0.29 |
| distance to cover | 0.014 ± 0.039 | 0.36 | 0.73 |
| group size | 0.033 ± 0.26 | 0.12 | 0.90 |
| Flight Movement Distance | | | |
| intercept (ACA) | 26.4 ± 2.46 | 10.7 | < 0.0001 |
| site (DHR) | 52.6 ± 4.08 | 12.9 | < 0.0001 |
| distance to settlement | 0.038 ± 0.011 | 3.47 | 0.007 |
| distance to trail | 0.038 ± 0.011 | 3.27 | 0.009 |
| group size | 0.25 ± 0.11 | 2.29 | 0.047 |
| proportion males | -4.16 ± 10.4 | 0.39 | 0.70 |
| distance to cover | -0.002 ± 0.021 | 0.11 | 0.91 |

rather than the effects directly resulting from legal trophy hunting). Another factor to consider is the effects of COVID-19 pandemic, which resulted in the disruption of legal hunting in DHR in 2020 and 2021 (NTNC, 2022). Thus, it is possible our findings may understate the actual impact of trophy hunting on the behaviour of blue sheep, because legal hunting pressure was reduced prior to our study (it is known that the behaviour of trophy hunted animals can change between hunting and non-hunting periods; Muposhi et al., 2016). However regardless of these caveats, the results are nonetheless an important reminder that the impacts of tourism activities can be multi-dimensional, and may have wider implications for tourism management beyond direct impacts on wildlife sex-ratios and population dynamics.

Currently, the DHR management plan recommends considering an expansion of the tourism potential for the area, and to develop 'sustainable eco-tourism' while maintaining the current focus on trophy hunting (DHR, 2019). While multi-use approaches to conservation areas are globally common, there is often little consideration of how different tourism experiences may conflict with each other. Our results suggest that even if current trophy hunting does not pose a direct threat to the viability of local Blue Sheep populations in the DHR (Karki and Thapa, 2013), it might inflict indirect costs to other tourism enterprises via its impact on animal behaviour. Tourist satisfaction when observing wildlife is at least partly related to how close animals can be approached and viewed without disturbance (Verbos et al., 2018). If Blue Sheep in the DHR are more vigilant, more easily disturbed at a longer approach range (>FID), and tend to flee longer distances when disturbed (>FMD), this complicates calculations relating to the viability of integrating eco-tourism operators for wildlife viewing into areas that also support trophy hunting activities. Our results also show that these tourism conflicts arising from changes in animal behaviour may not be uniform across the entire range of the focal species. In our study, Blue Sheep showed lower vigilance and reduced flight distances in areas closer to human settlements, an effect believed related to habituation (Stankowich, 2008); thus, it may be possible to limit hunting-eco-tourism conflicts in some viewing areas. Such conflict mitigation may also be managed by limiting eco-tourism activities to non-hunting periods when the animals may react less to the presence of people (e.g. Muposhi et al., 2016). However, it is uncertain how effective such a strategy would be.

## 5. Conclusions

Such potential for conflicts and interactions between wildlife tourism activities clearly suggests that targeted research or adaptive management approaches be used to identify how to best integrate tourism approaches in multi-use conservation areas. These issues are not restricted to Nepal or Blue Sheep conservation, but can be applied more broadly to many conservation and wildlife tourism management questions around the world. Animal behaviour is often overlooked as a key component of an integrated management approach for conservation of wildlife species (Clemmons and Buchholz, 1997; Berger-Tal et al., 2011). Yet it is the individual behavioural responses of animals to how they are managed that helps us predict the impacts of anthropogenic disturbance on wildlife populations (Caro and Berger, 2019). Ultimately this can be used by conservation managers to improve the status and experiences of both the wildlife that needs protection, and the tourists who help motivate and finance local conservation actions. Our results provide a snapshot of such effects, and suggest a need to examine how such conflicts that arise from behavioural responses to different tourist activities relate to spatial and temporal gradients within managed areas. For the Dhorpatan Hunting Reserve, managers should consider separating trophy hunting and eco-tourism in time and space, to minimise potential conflicting behavioural responses of individual animals on those tourism enterprises. This is important not only for species conservation in this case, but also for the development of sustainable and complementary wildlife tourism to financially support local conservation efforts.

## Statement of Ethics

This study was conducted according to the National Parks and Wildlife Conservation Act 1973, and National Parks and Wildlife Conservation Rules 1974. Permit No. 078/79 E/65.

## 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.

## Data Availability

Data will be made available on request.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02317.

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