

Road proximity and traffic flow perceived as potential predation risks: evidence from the Tibetan antelope in the Kekexili National Nature Reserve, China

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Abstract

Context. The risk-disturbance hypothesis predicts that animals exhibit risk-avoidance behaviours when exposed to human disturbance because they perceive the disturbance as a predatory threat.

Aims. This study aimed to examine whether Tibetan antelopes (*Pantholops hodgsoni*) exhibit risk-avoidance behaviour with proximity to a major highway and with increasing traffic flow consistent with the risk-disturbance hypothesis.

Methods. Focal-animal sampling was used to observe the behaviour of Tibetan antelopes. The behaviours were categorised as foraging, vigilance, resting, moving, or other. The time, frequency, and duration of foraging and vigilance were calculated.

Key results. As distance from the road increased, time spent foraging and foraging duration increased while foraging frequency, time spent being vigilant and vigilance frequency decreased, indicating that there is a risk perception associated with roads. Tibetan antelopes presented more risk-avoidance behaviours during high-traffic periods compared with low-traffic periods.

Conclusions. Tibetan antelopes exhibited risk-avoidance behaviour towards roads that varied with proximity and traffic levels, which is consistent with the risk-disturbance hypothesis.

Implications. The consequences of risk-avoidance behaviour should be reflected in wildlife management by considering human disturbance and road design.

Introduction

The potential impacts of human disturbance on wildlife are widely studied in conservation biology (Forman and Alexander 1998; Duchesne *et al.* 2000; Trombulak and Frissell 2000; Wakefield and Attum 2006; Reimers *et al.* 2007). Human disturbance can be caused by human or human-related presence, objects (e.g. pedestrians, cyclists, motorised vehicles, highways, railways, pipelines), or sounds (e.g. chasing, whistling). Such disturbances can cause aversion or stress in animals (Murphy and Curatolo 1987; Dyck and Baydack 2004; Reimers *et al.* 2007; Martin and Réale 2008). The risk-disturbance hypothesis predicts that animals exposed to human disturbance will exhibit risk-avoidance behaviours such as particular flight responses or avoiding certain habitats (Frid and Dill 2002). These behaviours are elicited because animals perceive the disturbance as a predatory threat (Gavin and Komers 2006). Disturbance and predation risk indirectly affect survival and reproduction through trade-offs between perceived risk and energy intake (Andrews 1990; Underhill and Angold 2000). If the disturbances, hunting pressure, or collision with vehicles increase the mortality of animals (Orłowski and Nowak

2006), then the behavioural responses of individuals' vigilance levels, fleeing response, or movement patterns, will be stronger (Forman and Alexander 1998; Trombulak and Frissell 2000).

Tibetan antelopes (*Pantholops hodgsonii*) are endemic to the Qinghai–Tibet Plateau of western China (Schaller 1998). They are classified as endangered by the International Union for Conservation of Nature (IUCN 2010), and listed in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) because of illegal hunting for both meat and underwool. Previous field surveys demonstrated a migratory route of Tibetan antelopes from the southern winter range in Qumalai County to the northern lambing grounds within the Kekexili National Nature Reserve (KNNR) near Zhuonai Lake (Schaller 1998; Lian *et al.* 2005). This migratory route crosses the Qinghai–Tibet Highway (QTH, Xining–Lhasa section of No. 109 National Trunk Highway), which is the major transport route between the Tibetan Autonomous Region and the rest of China. In late May, adult and yearling female antelopes gather into migratory groups numbering in the hundreds and cross the QTH to lambing grounds, and then return with lambs in early August (Lian

et al. 2005, Lian *et al.* 2007). The migratory period coincides with the busiest time for vehicles on the QTH. The maximum traffic flow can reach up to 276 vehicles per hour. Observations suggest that the QTH may limit the movement of Tibetan antelopes because of the high volume of traffic.

Based on the risk-disturbance hypothesis, understanding the behavioural response of Tibetan antelopes to road traffic is important to predict the consequences of such human disturbance for threatened Tibetan antelopes. In this paper, varying distances from the QTH and the levels of traffic were used to identify potential differences in risk assessment. We measured changes in the behaviour of Tibetan antelopes to determine whether their responses are consistent with the risk-disturbance hypothesis.

Materials and methods

Study site

The study was conducted between No. 2970 milestone (93°25'E, 35°21'N) and Wudaoliang (93°05'E, 35°14'N), ~34 km along the QTH, which was built in the 1950s and marks the boundary between KNNR (89°25'–94°05'E, 34°19'–36°16'N) and the Sanjiangyuan National Nature Reserve (89°24'–102°23'E, 31°39'–36°06'N) (Fig. 1). The QTH transports ~85% of imports and ~90% of exports from the Tibetan Autonomous Region (TAR) and plays an important role in Tibetan economic development. Recently, two alternative transport routes into TAR, the Sichuan–Tibet Highway and the Xinjiang–Tibet Highway, were closed during periods of the year because of severe weather and poor road conditions. This resulted in increased traffic volume on the QTH due to rerouting of vehicles from Sichuan and Xinjiang. Human presence on the QTH is mainly associated with traffic and routine road maintenance because no residents live in the area.

The QTH runs parallel to the Qinghai–Tibet railway track. Tibetan antelopes are accustomed to the railway due to wildlife underpasses (Yang and Xia 2008). For example, 98.17% of 2952 antelopes crossed the railway by using the wildlife underpasses

in 2006. However, no wildlife passage is found on the QTH. To decrease the possible effects of railways or trains, we conducted behavioural observations in areas in which there are no railways.

The area has an average altitude of 4620 m, with no human settlement. The average temperature is -5.6°C , with a mean maximum temperature in July of 12.1°C and a mean minimum temperature in January of -23.7°C . Approximately 69% of the total precipitation (262.2 mm) falls during the short summer season (June–August) (Zhang 1996). Vegetation in the area is dominated by *Stipa purpurea*, *Carex moorcroftii*, *Oxytropis densa*, *Oxytropis falcate*, *Astragalus densiflorus*, *Astragalus confertum* and *Pleurospermum hedinii* (Guo 1996). A quadrat method was used to estimate the biomass of aboveground plants (Lian *et al.* 2007) in 2003 and 2010. There was no difference between 2003 and 2010 in the biomass of graminoids, the main food of Tibetan antelopes (Cao *et al.* 2008): 6.07 ± 1.39 (mean \pm 1 s.e.) g m^{-2} in 2003 (Lian *et al.* 2007) and 6.56 ± 1.13 g m^{-2} in 2010 (unpubl. data) ($P > 0.05$). Wild ungulates in the area included Tibetan antelopes, Tibetan gazelles (*Procapra picticaudata*), kiangs (*Equus kiang*), and wild yaks (*Bos grunniens*) (Zheng 1994). The most significant mammalian predator of the Tibetan antelope is the wolf (*Canis lupus*). Large raptors, including upland buzzards (*Buteo hemillasius*), cinereous vultures (*Aegypius monachus*), and lammergeyers (*Gypaetus barbatus*) are frequent scavengers of dead antelopes and other carrion (Lian *et al.* 2007). Moreover, vehicular traffic sometimes results in mortality while ungulates cross the QTH. During the study, Tibetan antelopes or Tibetan gazelles were killed by motor vehicles on 15 occasions.

Observation of antelope behaviour

Behavioural observations were carried out by focal-animal sampling along the QTH using binoculars (70 \times 10 magnification) and dictated via MP3 voice recorder (Altmann 1974) between 0800 and 2000 hours from 4 July to 4 September

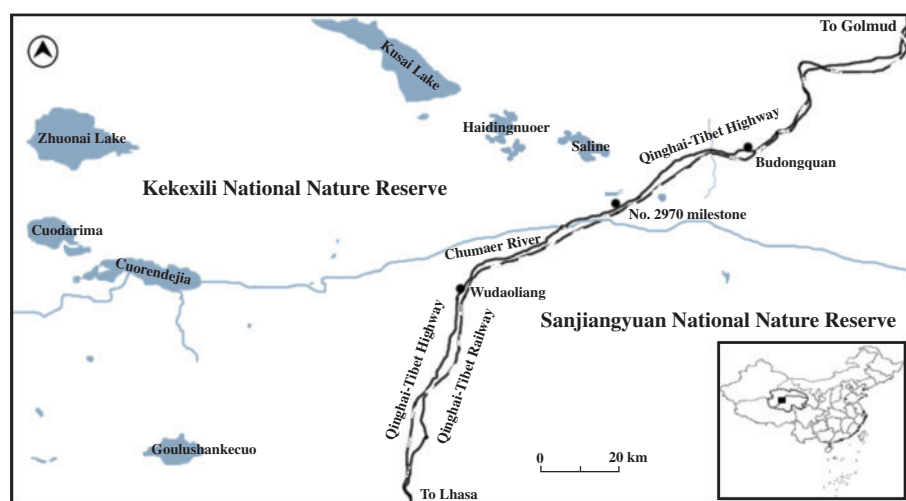


Fig. 1. Map of the study area. The study was conducted between No. 2970 milestone and Wudaoliang along the Qinghai–Tibet Highway (QTH) and in areas with no railways to decrease the possible effects of railways and trains.

2003 and 10 to 29 June 2010. A focal antelope was randomly selected along the QTH because it was difficult to distinguish individuals in the wild (e.g. using unique characteristics). The observers sheltered themselves in or behind the vehicle to reduce possible disturbance effects on antelopes while observing. One to four individuals were observed in each group. Groups at a particular location were revisited on subsequent days if the group had more than 10 individuals. By focusing on means, the samples (479 individuals) did not include significant unintended replication.

At the beginning of each observation, the date, time of day, location, distance to road, group size, and the presence of lambs were recorded. The distance of the focal animal from the road was measured using a laser range finder WCJ-2 (maximum range 6000 m). The road-effect zone averaged ~600 m in width (Forman and Deblinger 2000). Thus, the distance between the focal antelope and the QTH was limited to 1000 m and classified into one of six categories: ≤ 100 , 101–200, 201–300, 301–400, 401–500, and >500 m. A group was defined as a number of individual antelopes, excluding lambs, with a nearest-neighbour distance of less than 10 m. The locations of the focal antelopes in the group were marked as edge, centre-edge, or centre (Burger *et al.* 2000). Hundreds of antelopes scattered along the QTH during the migratory period and an overwhelming majority were classified as edge. Focal antelopes were classified into two social categories: female with lamb (mother) and female without (female). General vehicle numbers were noted on the QTH during behavioural observations by one observer. Three categories of traffic level were designated: low (≤ 40 vehicles/h), medium (60–80 vehicles/h), and high (≥ 100 vehicles/h).

Each focal individual was observed for 600 s. Data were omitted if the focal individual moved irretrievably out of view or if the focal animal was disturbed by unexpected factors (such as wolves present or tourists cheering and taking photos). All behaviours were classified into five categories: foraging, vigilance, resting, moving, or other activities. Tibetan antelopes were considered to be foraging when they stood with their head below shoulder level. Vigilance was defined as antelopes standing with their head at or above shoulder level. Resting referred to lying down on the ground. Walking or running with their head above shoulder level was recorded as moving. Other behaviours included drinking, excreting, tickling, grooming, playing, and nursing a lamb. All recorded data were processed using EthoLog 2.2 (Ottoni 2000) by the same observer (X. Lian).

Data analysis

Each focal-animal sample (i.e. each 600 s observation bout) was used as one data unit in all statistical tests. A total of 479 units were recorded. In each 600 s observation we calculated the: total 'time spent foraging'; number of separate foraging bouts (the 'frequency'); and the 'duration' (time spent foraging divided by the frequency of foraging). The total time, frequency, and duration of vigilance were calculated in a similar manner.

Statistical analyses were performed using SPSS Statistics 19.0 (IBM Corporation, New York). Data were first subjected to a Kolmogorov–Smirnov test of normality. As they did not show a normal distribution ($P < 0.001$), the data were then

transformed using Box–Cox transformation and Johnson transformation, but still failed to show a normal distribution. Thus, non-parametric tests were used. Medians and inter-quartile ranges were also calculated.

Mann–Whitney U tests were used to demonstrate differences when comparing foraging and vigilance between mother and female antelopes. Kruskal–Wallis H tests were used to determine differences in time, frequency, or duration of foraging and vigilance among the six distance categories. Spearman's rank correlation coefficients were used to assess the correlations between distance to the QTH and foraging (or vigilance). Vigilance and foraging times were examined using a correlation analysis to test whether there were trade-offs between the two behaviours. In all cases, P -values < 0.05 were considered statistically significant.

Results

Effects of road proximity on foraging

The median time spent foraging, frequency of foraging, and duration of foraging bouts in 600 s focal-antelope sampling bouts were 423.43 s (99.88–586.53), 2.22 events (0.91–4.20), and 126.59 s (60.50–295.51), respectively. Kruskal–Wallis H tests showed that the time ($\chi^2 = 16.890$, $df = 5$, $P < 0.01$; Fig. 2a), frequency ($\chi^2 = 35.548$, $df = 5$, $P < 0.01$; Fig. 2b), and duration ($\chi^2 = 28.020$, $df = 5$, $P < 0.01$; Fig. 2c) of foraging varied significantly among the six road proximity categories. Tibetan antelopes showed a significant trend of increased foraging time ($R_s = 0.140$, $P < 0.01$) and duration ($R_s = 0.228$, $P < 0.01$) when individuals were located further away from the road than when they were close to the road, regardless of traffic level, but the foraging frequency was in opposition ($R_s = -0.128$, $P < 0.01$). Foraging time ($P < 0.05$) and duration ($P < 0.01$) appeared to be higher in the low-traffic than in the high-traffic period.

Effects of road proximity on vigilance

The median time, frequency, and duration of vigilance in Tibetan antelopes were 6.61 s (0.27–50.88), 1.04 events (0.18–3.02), and 11.97 s (5.98–23.68), respectively. As distance from the QTH increased, vigilance time ($P < 0.01$) and frequency ($P < 0.01$) significantly decreased and varied among the six road proximity categories ($P < 0.01$; Fig. 3). Tibetan antelopes were more vigilant in high-traffic periods, exhibiting increased time spent ($P < 0.01$) and greater frequency ($P < 0.01$) of vigilance than in other periods.

Trade-off between foraging and vigilance and the group composition

Vigilance and foraging were negatively correlated with each other (Spearman's rank correlation, $R_s = -0.337$, $P < 0.001$), suggesting a trade-off (Fig. 4). There were no differences in foraging and vigilance between mothers and females ($P > 0.05$) and the two behaviours were not influenced by varying distances from the QTH when the lambs were present ($P > 0.05$).

Discussion

In this study, behavioural changes in Tibetan antelopes were observed at different intensities of human disturbance, based on

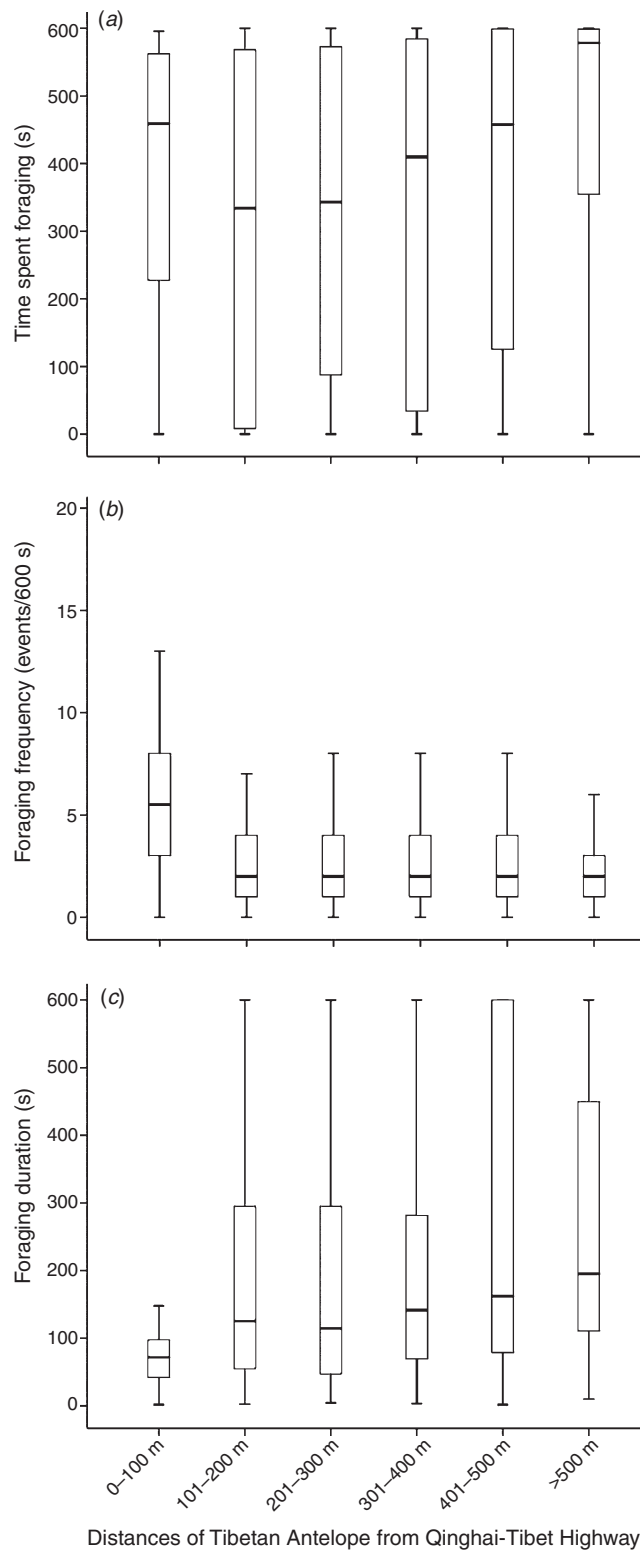


Fig. 2. Variance of time spent foraging in Tibetan antelope. (a) Foraging frequency, (b) foraging duration, (c) with varying proximity to the road.

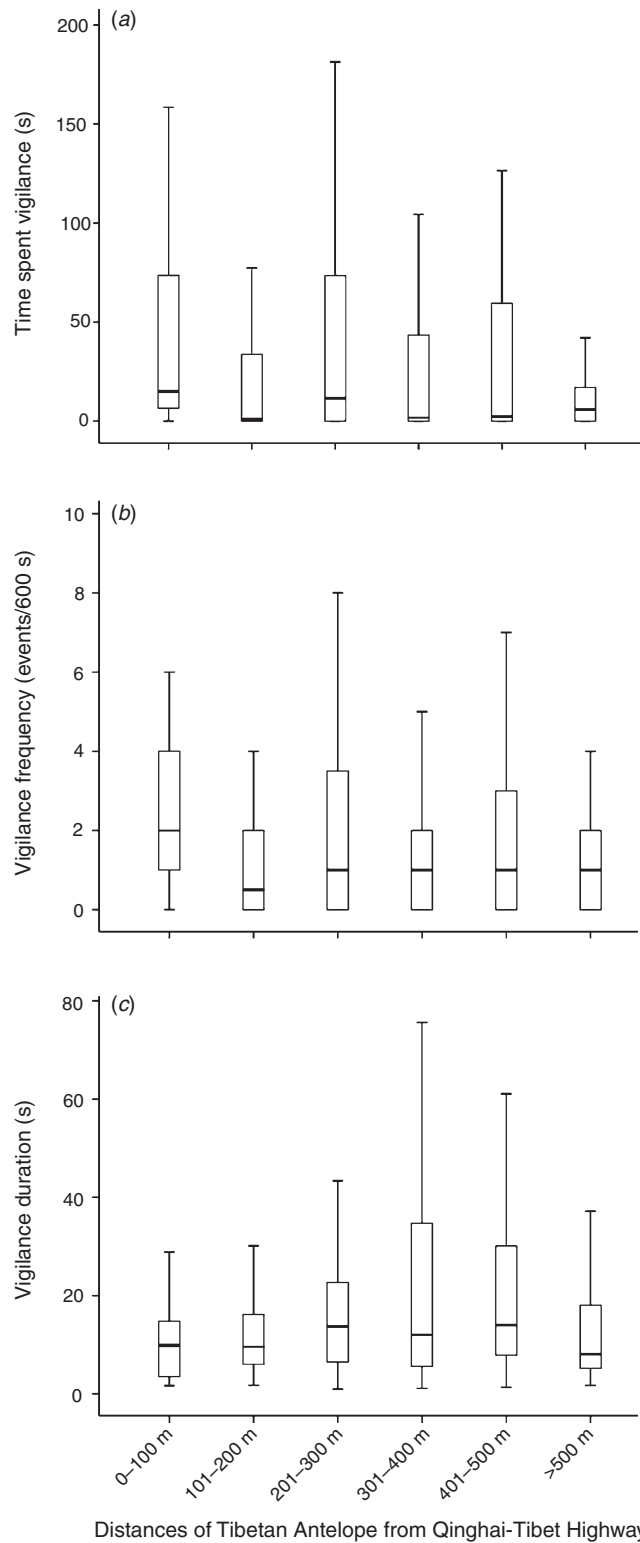


Fig. 3. Variance of time spent in vigilance in Tibetan antelope. (a) Vigilance frequency, (b) vigilance duration, and (c) with varying proximity to the road.

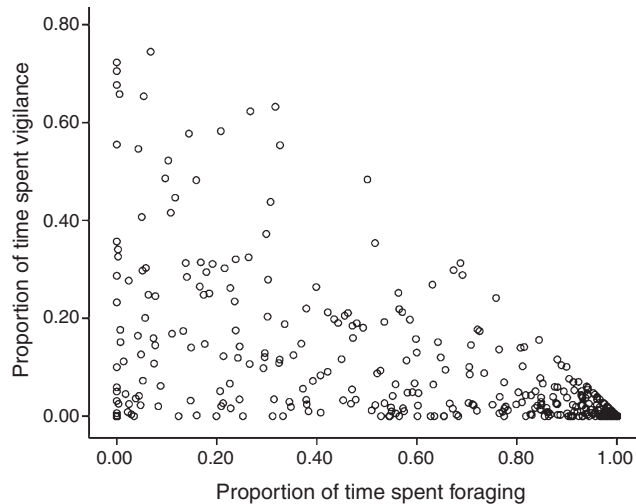


Fig. 4. Trade-off between foraging and vigilance in Tibetan antelopes.

road proximity and traffic levels. Human disturbance effects on foraging and vigilance behaviours in Tibetan antelopes were considered analogous to patterns observed under natural predation risk. Foraging and vigilance are assumed to contribute to the survival and breeding of ungulates inhabiting open rangelands (Goldsmith 1990). If the predation risk of the environment is high, Tibetan antelopes can enhance their vigilance level and actively evade risk. In this study, increased distance from a road increased foraging time and duration, but significantly decreased foraging frequency and the time and frequency of vigilance, regardless of traffic level. The risk-avoidance behaviour in Tibetan antelopes was higher near roads, suggesting an overall perception of risk towards roads. One possibility for these distance effects may be attributed to more open study areas. For example, Soay sheep (*Ovis aries*) on Lundy Island are more vigilant on the slopes than on the plateau, which could be explained by greater visibility on the plateau (Hopewell *et al.* 2005).

Here, Tibetan antelopes spent less time foraging and were more vigilant in high-traffic periods, which suggests that Tibetan antelopes perceive road traffic as a predatory threat. A similar effect has been noted in pronghorns (*Antilocapra americana*), which perceive roads with less traffic as a lower predation risk (Gavin and Komers 2006), and consequently decrease vigilance by scanning less frequently, for shorter periods, or both (Goldsmith 1990). White-tailed deer (*Odocoileus virginianus*) were forced to use alternative habitats when areas visible from the road were disturbed by high volumes of traffic and human activity. Conversely, bighorn sheep were not affected by traffic, possibly because areas they use are out of sight of the road (Pelletier 2006).

Higher volumes of traffic may be perceived with higher predation risk because of increased human activity. During our study, tourists tried to walk up to Tibetan antelopes, and disturbed the natural behaviours of antelopes almost daily. Although we discarded the behavioural observations in which direct human contact or other unexpected factors occurred, human disturbances such as chasing, shouting, photographing or whistling are likely to have indirect consequences on Tibetan

antelopes. Indirect effects may also be induced by the noise of traffic. Stockwell *et al.* (1991) studied the effects of helicopter noise on activity time budgets in bighorn sheep and found that during winter, bighorn sheep were more sensitive to noise while the helicopter was flying at a lower altitude. In northern Alaska, Murphy and Curatolo (1987) found that caribou at disturbed sites had significantly different activity budgets than undisturbed caribou, and that disturbance effects were significantly greater at sites with traffic. Similarly, Tibetan antelopes may associate road traffic with human presence, and consequently, with risk of predation.

In general, females with young tend to have higher vigilance levels than females without young because young are vulnerable to predation (Childress and Lung 2003; Wolff and Horn 2003; Li *et al.* 2009). However, in this study, no behavioural differences were detected between mothers and females, and the presence or absence of lambs did not affect foraging or vigilance behaviour, regardless of distance from the QTH. During the migratory period (i.e. lambing season), hundreds of female antelopes gathered in the migratory corridors and group size effects were present. Increased detection ability and numerical dilution of risk in larger groups provides more protection for foragers, commonly resulting in more foraging and less vigilance (Elgar 1989; Delm 1990; Roberts 1996; Lian *et al.* 2007). Moreover, the combination of low biomass of graminoids (~10% of total biomass), short growing season of herbage, and presence of competing herbivore species may result in severe food competition, which is exacerbated during migration (Lian *et al.* 2007). Thus, mothers must decrease time spent being vigilant due to increased foraging requirements needed to compensate for higher energy depletions of nursing lambs.

Management implications

Tibetan antelopes exhibited less risk-avoidance behaviour in areas with low human disturbance, such as those further away from the road and during times of low traffic. Controlling human activity during the migratory period may assist safe crossing of Tibetan antelopes across the QTH. For example, implementing traffic control while antelopes approach the QTH. Furthermore, strengthening public education through media and erecting caution signs may help reduce disturbance to antelopes.

Wildlife crossings or underpasses could help alleviate the impacts of human disturbance on Tibetan antelopes. Many studies have evaluated the use of wildlife crossing structures (Ng *et al.* 2004; Gagnon *et al.* 2007). Monitoring and evaluating the crossing structures of the Qinghai–Tibet railway showed that bridges that allow wildlife to pass below are the best type of wildlife passage (Xia *et al.* 2007). Similarly, bridges may be the most suitable type of wildlife passage for the highway in this study. Inspection of the local topography suggested that bridges could be built over several bottomlands, which could reduce the negative effects of human activities on Tibetan antelopes and help them cross QTH under bridges.

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References

- Altmann, J. (1974). Observational study of behaviour: sampling methods. *Behaviour* **49**(3), 227–266. doi:10.1163/156853974X00534
- Andrews, A. (1990). Fragmentation of habitat by roads and utility corridors: a review. *Australian Zoologist* **26**(3, 4), 130–141.
- Burger, J., Safina, C., and Gochfeld, M. (2000). Factors affecting vigilance in springbok: importance of vegetative cover, location in herd, and herd size. *Acta Ethologica* **2**, 97–104. doi:10.1007/s102119900013
- Cao, Y., Su, J., Lian, X., Zhang, T., and Cui, Q. (2008). Food habits of Tibetan antelope (*Pantholops hodgsoni*) in the Kekexili Nature Reserve. *Acta Theriologica Sinica* **28**(1), 14–19.
- Childress, M. J., and Lung, M. A. (2003). Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? *Animal Behaviour* **66**(2), 389–398. doi:10.1006/anbe.2003.2217
- Delm, M. (1990). Vigilance for predators: detection and dilution effects. *Behavioral Ecology and Sociobiology* **26**(5), 337–342. doi:10.1007/BF00171099
- Duchesne, M., Côté, S., and Barrette, C. (2000). Responses of woodland caribou to winter ecotourism in the Charlevoix Biosphere Reserve, Canada. *Biological Conservation* **96**(3), 311–317. doi:10.1016/S0006-3207(00)00082-3
- Dyck, M., and Baydack, R. (2004). Vigilance behaviour of polar bears (*Ursus maritimus*) in the context of wildlife-viewing activities at Churchill, Manitoba, Canada. *Biological Conservation* **116**(3), 343–350. doi:10.1016/S0006-3207(03)00204-0
- Elgar, M. A. (1989). Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Reviews of the Cambridge Philosophical Society* **64**(1), 13–33. doi:10.1111/j.1469-185X.1989.tb00636.x
- Forman, R., and Alexander, L. (1998). Roads and their major ecological effects. *Annual Review of Ecology and Systematics* **29**, 207–231. doi:10.1146/annurev.ecolsys.29.1.207
- Forman, R. T. T., and Deblinger, R. D. (2000). The ecological road-effect zone of a Massachusetts (USA) suburban highway. *Conservation Biology* **14**(1), 36–46. doi:10.1046/j.1523-1739.2000.99088.x
- Frid, A., and Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* **6**(1), 11.
- Gagnon, J., Theimer, T., Dodd, N., Manzo, A., and Schweinsburg, R. (2007). Effects of traffic on elk use of wildlife underpasses in Arizona. *The Journal of Wildlife Management* **71**(7), 2324–2328. doi:10.2193/2006-445
- Gavin, S., and Komers, P. (2006). Do pronghorn (*Antilocapra americana*) perceive roads as a predation risk? *Canadian Journal of Zoology* **84**(12), 1775–1780. doi:10.1139/Z06-175
- Goldsmith, A. (1990). Vigilance behavior of pronghorns in different habitats. *Journal of Mammalogy* **71**(3), 460–462. doi:10.2307/1381961
- Guo, K. (1996). Vegetation. In 'Physical Environment of Hoh Xil Region, Qinghai'. (Eds B. Li, G. Gu and S. Li.) pp. 100–118. (Science Press: Beijing.)
- Hopewell, L., Rossiter, R., Blower, E., Leaver, L., and Goto, K. (2005). Grazing and vigilance by Soay sheep on Lundy island: influence of group size, terrain and the distribution of vegetation. *Behavioural Processes* **70**, 186–193. doi:10.1016/j.beproc.2005.04.009
- IUCN (2010). IUCN Red List of Threatened Species. Version 2010.4. Available at <http://www.iucnredlist.org> [accessed 19 December 2010].
- Li, Z., Jiang, Z., and Beauchamp, G. (2009). Vigilance in Przewalski's gazelle: effects of sex, predation risk and group size. *Journal of Zoology* **277**, 302–308. doi:10.1111/j.1469-7998.2008.00541.x
- Lian, X., Su, J., Zhang, T., and Cao, Y. (2005). The characteristics of social groups of the Tibetan antelope (*Pantholops hodgsoni*) in the Kekexili region. *Acta Ecologica Sinica* **25**(6), 1341–1346.
- Lian, X., Zhang, T., Cao, Y., Su, J., and Thirgood, S. (2007). Group size effects on foraging and vigilance in migratory Tibetan antelope. *Behavioural Processes* **76**, 192–197. doi:10.1016/j.beproc.2007.05.001
- Martin, J., and Réale, D. (2008). Animal temperament and human disturbance: implications for the response of wildlife to tourism. *Behavioural Processes* **77**(1), 66–72. doi:10.1016/j.beproc.2007.06.004
- Murphy, S., and Curatolo, J. (1987). Activity budgets and movement rates of caribou encountering pipelines, roads, and traffic in northern Alaska. *Canadian Journal of Zoology* **65**(10), 2483–2490. doi:10.1139/z87-375
- Ng, S., Dole, J., Sauvajot, R., Riley, S., and Valone, T. (2004). Use of highway undercrossings by wildlife in southern California. *Biological Conservation* **115**(3), 499–507. doi:10.1016/S0006-3207(03)00166-6
- Orłowski, G., and Nowak, L. (2006). Factors influencing mammal roadkills in the agricultural landscape of south-western Poland. *Polish Journal of Ecology* **54**(2), 283–294.
- Ottoni, E. B. (2000). EthoLog 2.2: a tool for the transcription and timing of behavior observation sessions. *Behavior Research Methods, Instruments, & Computers* **32**(3), 446–449. doi:10.3758/BF03200814
- Pelletier, F. (2006). Effects of tourist activities on ungulate behaviour in a mountain protected area. *Journal of Mountain Ecology* **8**, 15–19.
- Reimers, E., Dahle, B., Eftestøl, S., Colman, J., and Gaare, E. (2007). Effects of a power line on migration and range use of wild reindeer. *Biological Conservation* **134**(4), 484–494. doi:10.1016/j.biocon.2006.08.034
- Roberts, G. (1996). Why individual vigilance declines as group size increases. *Animal Behaviour* **51**(5), 1077–1086. doi:10.1006/anbe.1996.0109
- Schaller, G. B. (Ed.) (1998). 'Wildlife of the Tibetan Steppe.' (University Chicago Press: Chicago, IL.)
- Stockwell, C. A., Bateman, G. C., and Berger, J. (1991). Conflicts in national parks: a case study of helicopters and bighorn sheep time budgets at the grand canyon. *Biological Conservation* **56**(3), 317–328. doi:10.1016/0006-3207(91)90064-G
- Trombulak, S., and Frissell, C. (2000). Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* **14**(1), 18–30. doi:10.1046/j.1523-1739.2000.99084.x
- Underhill, J., and Angold, P. (2000). Effects of roads on wildlife in an intensively modified landscape. *Environmental Reviews* **8**(1), 21–39. doi:10.1139/er-8-1-21
- Wakefield, S., and Attum, O. (2006). The effects of human visits on the use of a waterhole by endangered ungulates. *Journal of Arid Environments* **65**(4), 668–672. doi:10.1016/j.jaridenv.2005.08.007
- Wolff, J. O., and Horn, T. V. (2003). Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. *Canadian Journal of Zoology* **81**(2), 266–271. doi:10.1139/z03-011
- Xia, L., Yang, Q., Li, Z., Wu, Y., and Feng, Z. (2007). The effect of the Qinghai–Tibet railway on the migration of Tibetan antelope *Pantholops hodgsonii* in Hoh-xil National Nature Reserve, China. *Oryx* **41**(3), 352–357. doi:10.1017/S0030605307000116
- Yang, Q., and Xia, L. (2008). Tibetan wildlife is getting used to the railway. *Nature* **452**(7189), 810–811. doi:10.1038/452810c
- Zhang, L. (1996). Climate. In 'Physical Environment of Hoh Xil region, Qinghai'. (Eds B. Li, G. Gu and S. Li.) pp. 16–46. (Science Press: Beijing.)
- Zheng, S. (Ed.) (1994). 'Fauna of Rare and Endangered Species of Vertebrates in Northwest China.' (China Forestry Publishing: Beijing.)

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