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Behavioural Processes 76 (2007) 192–197

BEHAVIOURAL PROCESSES

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Group size effects on foraging and vigilance in migratory Tibetan antelope

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Received 26 July 2006; received in revised form 26 March 2007; accepted 12 May 2007

Abstract

Large group sizes have been hypothesized to decrease predation risk and increase food competition. We investigated group size effects on vigilance and foraging behaviour during the migratory period in female Tibetan antelope *Pantholops hodgsoni*, in the Kekexili Nature Reserve of Qinghai Province, China. During June to August, adult female antelope and yearling females gather in large migratory groups and cross the Qinghai–Tibet highway to calving grounds within the Nature Reserve and return to Qumalai county after calving. Large groups of antelope aggregate in the migratory corridor where they compete for limited food resources and attract the attention of mammalian and avian predators and scavengers. We restricted our sampling to groups of less than 30 antelopes and thus limit our inference accordingly. Focal-animal sampling was used to record the behaviour of the free-ranging antelope except for those with lambs. Tibetan antelope spent more time foraging in larger groups but frequency of foraging bouts was not affected by group size. Conversely, the time spent vigilant and frequency of vigilance bouts decreased with increased group size. We suggest that these results are best explained by competition for food and risk of predation.

Keywords: Foraging; Group size; Kekexili nature reserve; Tibetan antelope; Vigilance

1. Introduction

For many species, especially birds and mammals, vigilance is traditionally considered to function predominantly for protection from predators (Roberts, 1996; Treves, 2000). Previous research has focused on the influence of predation risk on behavioural patterns at the individual level (Bednekoff and Lima, 1998b; Beauchamp and Ruxton, 2003). Animals typically tend to increase time spent vigilant and decrease time spent foraging when predation risk is high. If the predation risk is low, animals allocate their behavioural time budget according to other factors, such as group size and nutritional requirements (Hopewell et al., 2005).

Group-size effects in mammals and birds are most often studied by examining the trade-off on time allocated to antipredator vigilance and foraging (Elgar, 1989; Roberts, 1996; Treves, 2000; Beauchamp, 2001; Bednekoff and Lima, 1998a, 2004). Generally, animals in larger groups devote less time to vigilance and correspondingly more to foraging than those which are solitary (Pulliam, 1973; Caraco, 1979; Shorrocks and Cokayne, 2005). This finding can be interpreted in two different ways. First, a dilution effect exists so animals in larger groups are more likely to detect predators and are less likely to be killed than animals in smaller groups. As a result, individuals in larger groups can decrease their time spent on vigilance and increase their time foraging (Dehn, 1990; Lazarus, 2003; Beauchamp, 2003a). Second, competition for limited food resources is greater in large groups and thus individuals must compete by foraging more quickly than their companions (Clark and Mangel, 1986; Beauchamp, 2001, 2003a, 2003b).

Tibetan antelope (or chiru) *Pantholops hodgsoni* are endemic to the high-altitude Qinghai-Tibet Plateau of western China (Schaller, 1998). Historical accounts indicate that very large populations of Tibetan antelope ranged across an area of 2,500,000 km^2 in the early 20th century. Illegal hunting for both meat and wool resulted in major declines in abundance and distribution. Current population estimates of Tibetan antelope are ∼75,000 individuals and they are classified as endangered by IUCN (2001) and listed in Appendix I of CITES. The distribution of Tibetan antelope is now restricted to remote areas in the Tibetan autonomous region (TAR), Qinghai province and the Xinjiang autonomous region and the largest remaining

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doi:10.1016/j.beproc.2007.05.001

populations are found in the Chang Tang reserve of northern TAR and the adjacent Kekexili nature reserve (KNR) in Qinghai (Schaller, 1998).

Tibetan antelope are migratory across much of their range. Previous field surveys in western Qinghai have demonstrated that there is a traditional migratory route from the southern winter range in Qumalai county to northern calving grounds within the KNR near Zhuonai Lake (Schaller, 1998; Lian et al., 2005). Approximately 3000 female antelopes inhabit Qumalai county in an area of 47,000 km^2. In late June, adult and yearling females gather into migratory groups of up to 600 individuals and cross the Qinghai–Tibet highway to calving grounds near Zhuonai Lake and then return with lambs in early August (Lian et al., 2005). This period is critical for the antelope population because of the vulnerability of lambs to predators, the severe weather and the high energetic demands of migration, in addition to continuing problems of illegal hunting (Wong, 1998; Xi and Wang, 2004; Schaller et al., 2006).

The behaviour and ecology of Tibetan antelope has received little study, particularly during the migratory period (Schaller, 1998; Schaller et al., 2006). In this paper we examine the effect of antelope group size on foraging and vigilance behaviour during the migration.

2. Materials and methods

2.1. The study area

The study area is adjacent to the Qinghai–Tibet highway which forms the southeastern boundary of the KNR (34°19′-36°16′N, 89°25′-94°05′E) in Qinghai Province, China. The KNR, uninhabited by humans because of its remoteness, high elevation and harsh climate, occupies about 45,000 km^2 in western Qinghai Province on the border of the Tibetan autonomous region and the Xinjiang autonomous region. The average elevation is 4,600 m with a range from 4200 to 6860 m. The average annual temperature is −5.6 °C and 69% of total precipitation (262.2 mm) falls during June–August (Zhang, 1996).

The vegetation in the study area is primarily alpine grassland and alpine meadow dominated by *Stipa purpurea*, *Carex moorcroftii*, *Oxytropis densa*, *Oxytropis falcata*, *Astragalus densifolrus*, *Astragalus confertum* and *Pleurospermum hedinii* (Guo, 1996; Wu et al., 1996). A quadrat method was used to estimate the biomass of aboveground plants. Twenty 1-m^2 quadrats were sampled randomly from lightly grazed areas within the study area. For each quadrat, the percentage of ground covered by grass was estimated and biomass was clipped to ground level for all herbaceous species (annuals, or only the green of perennials), to represent the material grazed by the antelope. The clipped plant material was sorted into graminoids, sedges and forbs, weighed separately after 48 h of oven drying at 60 °C. The samples were thoroughly cleaned of any soil contamination before weighing. Vegetation cover was less than 20% and the biomass of graminoids, sedges and forbs were 6.07 ± 1.39 (mean ± 1 S.E.) g/m^2, 13.87 ± 5.39 g/m^2 and 30.23 ± 6.90 g/m^2, respectively.

Wild ungulates in KNR include Tibetan antelope, Tibetan gazelle *Procapra picticaudata*, kiang *Equus kiang* and wild yak *Bos grunniens* and are protected from hunting by national law (Schaller et al., 1991; Zheng, 1994). Domestic yak and sheep *Ovis aries* are herded by nomadic pastoralists in the study area. The most significant mammalian predator of Tibetan antelope within KNR is the wolf *Canis lupus*, which is relatively common, and the lynx *Felis lynx* and the brown bear *Ursus arctos*, which are much rarer. Large raptors including upland buzzard *Buteo hemillasius*, cinereous vulture *Aegypius monachus* and lammergeier *Gypaetus barbatus* are common in KNR and are frequent scavengers of dead antelope and other carrion.

2.2. Behavioural observations

We conducted this study during June 26–September 20, 2003 and June 25–September 26, 2004. Observations were made by focal-animal sampling (Altmann, 1974). Female antelopes with lambs were excluded to avoid the influence of parental duties on behaviour. We randomly selected focal animals and made direct observations with binoculars. For each observation, we noted the following variables: date, time, weather, group size (number of all adult individuals in a group) and the nearest-neighbour distance (using body length as an indication, Burger and Gochfeld, 1994; Burger et al., 2000). We defined a group as a number of individual antelope with nearest-neighbour distance of less than 10 m regardless of their behavioural state. Individuals that were more than 10 m from another antelope were not considered part of that group. Solitary individuals were considered groups of one. We recorded the behaviour of focal animals using Samsung voice recorders to ensure the accuracy of the behavioural data. We defined five behavioural categories: foraging, vigilant, resting, moving, and other activities (e.g., drinking, excreting, jumping, grooming and playing). Antelopes were categorized as foraging when they were standing with their head below shoulder level, biting or chewing vegetation, or if they were walking with their muzzle close to the ground. They were categorized as vigilant if they were standing while watching with the head at or above the shoulder level. Moving was defined as walking or running with their head at or above the shoulder level. Resting was recorded if the animal was lying down. Each observation bout lasted 600 s. To reduce the probability that the same individual was observed more than once, only one to four individuals were observed in each group, and groups at a particular location were revisited on subsequent days only if they contained more than 10 individuals. Observations were abandoned if the focal individual moved out of view and if the group varied in size.

2.3. Statistical analyses

Behavioural data were processed using EthoLog 2.2 (Ottoni, 2000). Accumulated time and frequency of behaviours were calculated and each focal animal sampling bout was used as one datum unit in statistical tests. We restricted our sampling to groups of 30 or fewer animals, and thus limited our inference accordingly. Group size was categorized as: 1, 2–5, 6–10, 11–15, 16–20, 21–25 and 26–30. Foraging and vigilance are the two primary factors influencing the survival and breeding of the migratory Tibetan antelopes because of the limited food resource and high predation risk in study area and thus the two behaviours were analysed as dependent variables. Behavioural data were not normally distributed (Kolmogorov–Smirnov tests for normality, $P < 0.001$ and Bartlett-Box F tests for homoscedasticity, $P < 0.05$), and therefore medians and inter-quartile ranges are used throughout the paper.

We used Kruskal–Wallis *H* tests to determine whether there were differences in time or frequency of foraging and vigilance among the seven group size categories. Spearman's rank correlation tests were used to analyse the correlations between group size and foraging (or vigilance). All statistical analyses were carried out using SPSS, v.11.5.

3. Results

3.1. Group size effects on foraging

We collected 178 focal observations from 112 groups of female Tibetan antelope. Animals spent a median 68.0% (range 20.7–97.8) of their time foraging and 1.7% (0.1–11.6) vigilant.

The median time foraging in each 600 s focal animal sampling bout was 408.2 (124.0–586.6) s. The antelopes characteristically devote more time to foraging as group size increases (Spearman's rank correlation test: $R_s = 0.154$, $n = 178$, $P < 0.05$; Fig. 1), and the time spent foraging differed in seven different group size categories (Kruskal–Wallis *H* test: $\chi^2 = 13.825$, $df = 6$, $P < 0.05$).

The median frequency of foraging bouts was 2.2 (0.9–4.2) times per 600 seconds and did not vary with the group size (Kruskal–Wallis *H* test: $\chi^2 = 9.362$, $df = 6$, $P > 0.05$). The correlation coefficient of Spearman's rank correlation test between the group size and frequency of foraging was −0.096, which is not significant ($n = 178$, $P > 0.05$; Fig. 2).

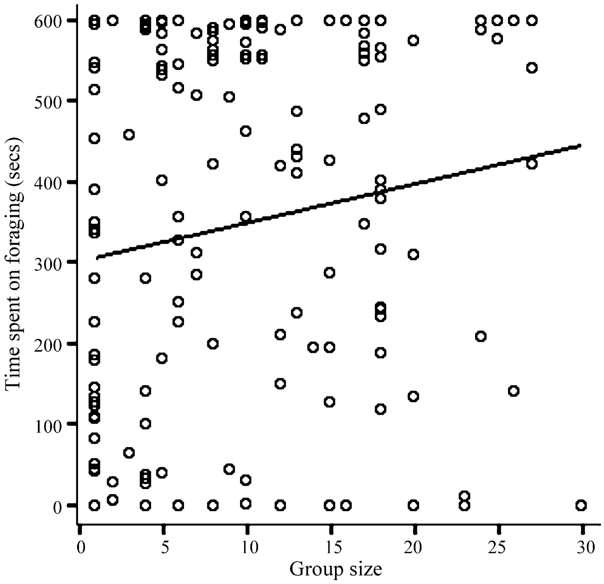

Fig. 1. Relationship between group size and time spent on foraging in migratory Tibetan antelope.

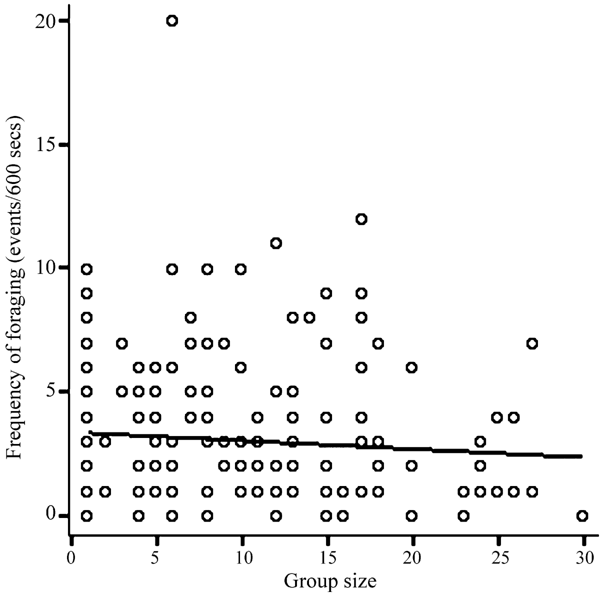

Fig. 2. Relationship between group size and frequency of foraging in migratory Tibetan antelope.

3.2. Group size effects on vigilance

The median time spent vigilant in Tibetan antelope was 10.4 (0.4–69.4) s. There was a negative correlation between group size and time spent on vigilance (Spearman's rank correlation test: $R_s = -0.276$, $n = 178$, $P < 0.01$; Fig. 3) and time of vigilance differed in seven different group size categories (Kruskal–Wallis *H* test: $\chi^2 = 14.550$, $df = 6$, $P < 0.05$).

The median of frequency of vigilance was 1.1 (0.2–3.6) times per 600 s. The Tibetan antelopes in larger groups were less vigilant than those in smaller groups (Spearman's rank correlation test: $R_s = -0.297$, $n = 178$, $P < 0.01$; Fig. 4). Frequency of vigi-

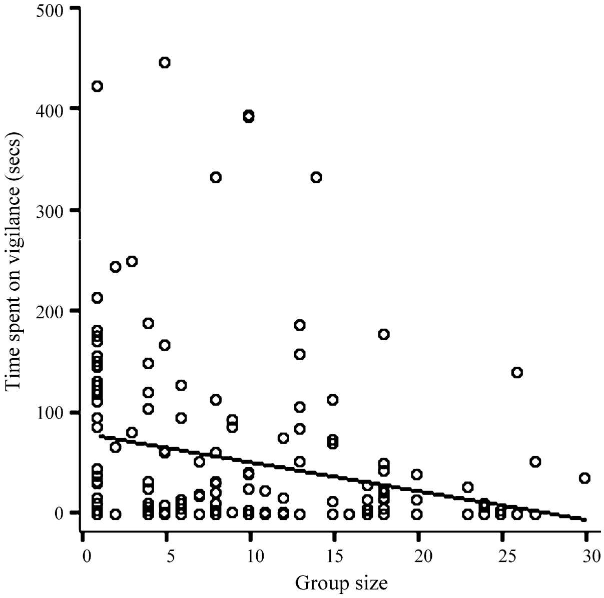

Fig. 3. Relationship between group size and time spent on vigilance in migratory Tibetan antelope.

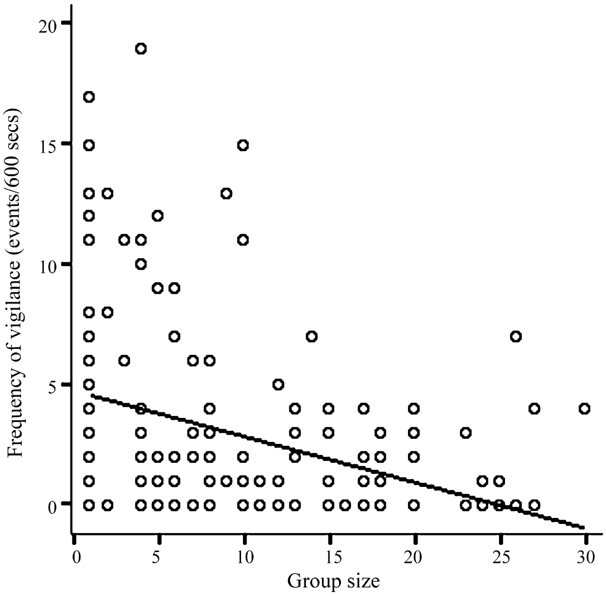

Fig. 4. Relationship between group size and frequency of vigilance in migratory Tibetan antelope.

lance differed significantly among seven group size categories (Kruskal–Wallis *H* test: $\chi^2 = 18.518$, $df = 6$, $P < 0.01$; Fig. 4).

4. Discussion

In common with most large herbivorous mammals, female Tibetan antelope in this study spent large amounts of their time foraging. Owen-Smith (1998) reported that female greater kudu *Tragelaphus strepsiceros* spent 63% of time foraging and temperature was the primary factor influencing the time budget. Scottish Blackface sheep *Ovis aries* spent over half of daylight hours foraging in order to obtain sufficient intake (Clarke et al., 1995) and a takh stallion *Equus ferus przewalskii* spent 47% of his time foraging (Boyd, 1998). The comparatively high foraging time budgets of Tibetan antelopes observed in this study may be a result of the high-energy demands of migration in the severe high-altitude climate of the Qinghai-Tibet Plateau (Lian et al., 2007). We also found a significant positive effect of group size on the time spent foraging and a significant negative effect of group size on time spent vigilant. Is competition for food or risk of predation more likely to be responsible for this relationship?

The aboveground biomass of vegetation in the KNR was very low. We found that vegetation cover during the period when it was being utilized by migrating antelope was less than 20% and the biomass production for graminoids, sedges and forbs were 6.07 ± 1.39, 13.87 ± 5.39 and 30.23 ± 6.90 g/m^2, respectively. Vegetation biomass in the KNR was slightly higher than that in the adjacent Chang Tang Reserve (27.7 ± 25.5 g/m^2; Schaller, 1998), but was considerably lower than that in African savannahs such as the Maasai Mara National Reserve (368–466 g/m^2) and Nairobi National Park (326–499 g/m^2) in Kenya (Boutton et al., 1988). Some areas of short-grass plains in the Serengeti National Park in Tanzania have a biomass of 84 g/m^2 despite being heavily grazed by high densities of migratory ungulates including wildebeest *Connochaetes taurinus*, zebra *Equus burchelli* and Thompson's gazelle *Gazella thomsoni* (McNaughton, 1979).

Based on microhistological analyses of faecal material, Schaller (1998) reported that the diets of Tibetan antelope, kiang, and wild yak consisted mainly of graminoids whilst Tibetan gazelle selected forbs. In a parallel study, we have obtained data on the summer diets of Tibetan antelope in KNR and compared these to other sympatric ungulates, including Tibetan gazelle, kiang, wild yak, domestic yak and domestic sheep (unpublished data). The results revealed that graminoids were the dominant food item of Tibetan antelope, accounting for 55.6% by volume. We used Schoener's (1970) index to quantify diet overlap between Tibetan antelope and the other sympatric ungulates. The highest diet overlap occurred between Tibetan antelope and domestic sheep (0.73), closely followed by kiang (0.63), wild yak (0.52), domestic yak (0.52), and finally Tibetan gazelle (0.33). Schoener's index is considered to indicate biologically significant competition for food when it exceeds 0.60 (Mathur, 1977), thus suggesting that domestic sheep and kiang may compete with Tibetan antelope for food resources.

The combination of the low biomass of graminoids (about 10% of the total biomass) and short growing season of herbage provide limited food resources for Tibetan antelope. These food resources are shared with a guild of sympatric large herbivores, several of which have very similar diets to Tibetan antelope. The combination of low biomass, short growing season and presence of competing herbivore species may result in severe food competition, which is exacerbated during the migration when thousands of female antelopes aggregate in the migratory corridor.

The large groups of antelope and the presence of lambs attracted the attention of mammalian predators, particularly wolves. Wolves are widespread and relatively common on the Qinghai-Tibet Plateau ascending as high as 5300 m (Schaller, 1998). Studies in the Chang Tang indicate that wolf diet is highly variable, being dominated by marmot *Marmota himalayana* and pika *Ochotona curzoniae* during the summer, but that Tibetan antelope can be seasonally very important particularly during the migration (Schaller, 1998). We directly observed Tibetan antelope being attacked and killed by wolves on 17 occasions. The migration of the antelope also attracted avian predators, in particular the upland buzzard, cinereous vulture and lammergeier, all of which were common in the KNR. Antelope appeared to form a significant component of the diet of at least some of these species during the migration. For example, we found 49 legs of antelope lambs in one nest of the upland buzzard in 2004 summer and DNA analyses showed that these legs were from 36 different individuals. It is most likely that these antelope lambs were scavenged by raptors after death from other causes (e.g. wolf predation or starvation). Large eagles have been observed to kill lambs elsewhere, and eagles have been killed by sheep farmers in many countries where sheep husbandry is practiced, however the available scientific evidence suggests that eagle predation is typically a small percentage of the overall mortality of lambs (Thirgood et al., 2005).

Foraging and vigilance are mutually exclusive activities and therefore a decrease in the time spent vigilant can potentially lead to an increase in time spent on foraging (Lima, 1987; McNamara and Houston, 1992; Frid, 1997). Our study supported this dynamic relationship in that individual antelope in larger groups spent more time foraging and less time vigilant. Furthermore, the balance between vigilance and foraging can tip towards foraging when food competition becomes more severe (Beauchamp and Ruxton, 2003). Vertebrate herbivores often undertake more foraging and less vigilance when in larger groups (Elgar, 1989; Quenette, 1990; McNamara and Houston, 1992; Roberts, 1996; Lima, 1995, 1998; Hunter and Skinner, 1998; Sun, 2001). For example, in springbok *Antidorcas marsupialis*, individuals in large groups foraged for significantly more time than individuals in small groups on the open, arid plains, which relate to the risk from predators and the benefits from other group members (Burger et al., 2000). Lagory (1986) suggested that the increase in foraging time in large groups of white-tailed deer *Odocoileus virginianus* was due to a reduction in vigilance. During this study, female Tibetan antelopes formed large, migratory groups and individual antelope may reduce their risk by foraging in larger group in which they can see all other individuals. Furthermore, the animals in groups were all at periphery of the group according to the definition of Burger et al. (2000) because we restricted our sampling to groups of 30 or fewer animals and the antelopes were scattered, so the dilution effect existed. Increased detection ability and numerical dilution of risk in larger groups might provide more protection to foragers, thus leading to more foraging and lower vigilance (Pulliam, 1973; Roberts, 1996; Barbosa, 2003; Bednekoff, 2003; Burger, 2003). Dehn (1990) found that vigilance of female elk *Cervus elaphus* was best explained by a model that included both benefits of dilution and detection. In addition, the larger groups of Tibetan antelope might bring greater competition for limited food and individual antelope might compensate by increasing the time spent foraging (Clark and Mangel, 1986; Beauchamp, 2003a; Bednekoff and Lima, 2004).

Acknowledgments

We would like to thank Richard B. Harris, Xuecong Liu and three anonymous referees for useful advice and comments on the manuscript. We also thank Mingcai Li, Yuanwen Duan, Lihua Meng and Jing Sun for their help. This study was funded by the State Key Technological Program of Qinghai Province of China (No. 2002-N-105) and the Knowledge Innovation Program of the Chinese Academy of Sciences (No. CXLY-2002-3). SJT's involvement was funded by an International Exchange Grant from the Royal Society of Edinburgh.

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