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Inter- and intraspecific vigilance patterns of two sympatric Tibetan ungulates

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Vigilance is an important antipredation technique that can be affected by many factors, such as body size and group size. Small animals are more vulnerable than large ones, so the former are expected to behave more vigilantly than the latter. This effect of body size on vigilance may occur inter- or intraspecifically. We studied the vigilance behavior of two sympatric wild ungulates, Tibetan antelopes (*Pantholops hodgsonii*) and Tibetan gazelles (*Procapra picticaudata*). Tibetan antelopes, with a body size of 33 kg are much larger than Tibetan gazelles, with a body size of approximately 14 kg. Tibetan antelopes are sexually and body-size dimorphic; that is, males are much heavier than females. Alternately, Tibetan gazelles are sexually dimorphic but the sexes do not differ in weight. Tibetan gazelles scanned their environment more frequently than Tibetan antelopes did. Small female Tibetan antelopes scanned their environment more frequently than males did, whereas male Tibetan gazelles scanned their environment more frequently than females did. Group size did not affect the vigilance of Tibetan gazelle, but its negative effect on the vigilance of male Tibetan antelopes was marginally significant. In female Tibetan antelopes, vigilance in large groups was high probably because of scramble competition and social monitoring. Our results suggested that body mass and group size play an important role in shaping the vigilance of these two rare Tibetan ungulates.

Key words: body-size principle, group-size effect, Tibetan antelope, Tibetan gazelle, vigilance

Vigilance is an antipredator behavior necessary for survival and reproductive success in nearly all kinds of animals (Hirschler et al. 2016), including various invertebrates (Injaian and Tibbetts 2015), fishes (Hess et al. 2016), amphibians (Martin et al. 2006), reptiles (Ito and Mori 2010), birds (Che et al. 2018), and mammals (Branstetter et al. 2018; Favreau et al. 2018; Welch et al. 2018). Vigilance is observed commonly when animals raise their heads to look around their surroundings (Beauchamp 2015). The most important function of vigilance is antipredation, which can help prey detect potential predators and adopt an appropriate response (Li 2016). Vigilance is also essential for monitoring social communication and resource or mate competition because of limitation of food, space within or between groups, and mates (Robinette and Ha 2001; Childress and Lung 2003; Cameron and Du Toit 2005; Beauchamp 2014).

Changes in vigilance behavior have been linked to many social and environmental factors (Roberts 1996; Li et al. 2009; Beauchamp 2015). Age, sex, reproductive status, and group size may influence vigilance behavior (Li et al. 2009, 2012, 2013; Couchoux and Cresswell 2012; Zheng et al. 2013). Increased predation risk or human disturbance also increases vigilance behavior (Wang et al. 2011; Zheng et al. 2013).

Vigilance behavior is affected by body size or adult body mass because antipredation ability may be size dependent, and small animals are more vulnerable than large animals (Beauchamp 2015). Thus, a larger, better-defended prey likely experiences a reduction in predation risk and consequently expresses a lower vigilance behavior. For instance, adult white rhinos (*Ceratotherium simum*) are giant herbivores with few natural enemies (Wang and Yang 2014; Penny et al. 2019), and show low vigilance except when accompanied by vulnerable young. This effect of body size on vigilance can occur both interspecifically and intraspecifically; that is, large sexually dimorphic males devote less time to being vigilant than their smaller female counterparts do. This effect has been observed in alpine ibex (*Capra ibex*—Brivio et al. 2014), but additional evidence should be obtained to confirm these hypotheses, especially for two or more coexisting species.

The negative relationship between group size and vigilance, namely, group-size effect, has been observed in many species (Pulliam 1973; Caraco 1979; Elgar 1989; Roberts 1996; Shorrocks and Cokayne 2005; Lian et al. 2007). At least three hypotheses have been proposed to explain the group-size effect. 1) The "more eyes and more ears" hypothesis or detection effect states that animals living in a large group can more easily detect potential predators and thus reduce their vigilance (Pulliam 1973). 2) The "safety in numbers" hypothesis suggests that animals living in a large group can benefit from dilution (Foster and Treherne 1981; Cresswell 1994). 3) The "scramble competition" hypothesis suggests that animals living in a large group have to compete with their group members for limited food resources, thus reducing their vigilance (Clark and Mangel 1986; Beauchamp and Ruxton 2003; Rieucau and Giraldeau 2009). However, the group-size effect does not occur in some species, such as giraffes (*Giraffa camelopardalis*—Cameron and Du Toit 2005).

We studied the vigilance behaviors of two sympatric ungulates, namely, Tibetan antelopes (*Pantholops hodgsonii*) and Tibetan gazelles (*Procapra picticaudata*), to explore if and how body size (interspecific and intraspecific) and group size affected vigilance. Tibetan antelopes are sexually dimorphic; that is, adult males with an average body weight of 39 kg are larger than females with an average of 26 kg (Leslie et al. 2008). Tibetan gazelles are also sexually dimorphic (Li and Jiang 2008). However, male and female gazelles have similar body sizes with an average of 14 kg (Leslie 2010). In Tibetan gazelles, group size ranged from one to nine. The group structure of Tibetan antelopes was different from that of Tibetan gazelles. The group size of male antelopes was small, usually no more than 20 individuals, but groups of females could be extremely large and reach a few hundred or thousands.

On the basis of the body-size hypothesis, we predicted that 1) the smaller Tibetan gazelles would be more vigilant than Tibetan antelopes, and 2) female Tibetan antelopes would show more vigilance than males, whereas male and female Tibetan gazelles would show no difference in vigilance. On the basis of the group-size hypothesis, we predicted that 3) vigilance will decrease as group size increases.

Materials and Methods

Study area.—This study was conducted in Shenzha County (30°02′39″–32°19′33″N, 87°45′30″–89°47′49″E), which is located in the central part of Qiangtang Plateau, Tibet. Its elevations range from 4,530 to 6,448 m with an average of 4,700 m. Its local climate is characterized by extreme cold and long winters, strong winds, and high levels of solar radiation. The mean annual temperature is 0.4°C. The annual precipitation is approximately 330 mm, and rain falls mostly between June and September. Alpine meadow is the main vegetation type, and no shrubs grow in the area.

Study species.—Tibetan antelopes and gazelles (Fig. 1) are two focal species that coexist in Selincuo National Nature Reserve, Shenzha County, Tibet. The reserve also commonly harbors mammalian predators, including wolves (*Canis lupus*), lynx (*Lynx lynx*), and brown bears (*Ursus arctos*), and large raptors, including upland buzzards (*Buteo hemilasius*) and cinereous vultures (*Aegypius monachus*). These rare ungulates may be increasingly threatened by feral dogs (*Canis familiaris*) that prey on local ungulates and birds (Yang et al. 2019).

Tibetan antelopes are a flagship species on the Qinghai–Tibet Plateau. They were poached heavily for their fine underfur, used to make high-quality shawls, thus endangering their survival (Schaller 1998). Tibetan antelopes have been classified as a category I (endangered in China) national protected wild animal species in China since 1989 and nearly threatened by the IUCN since 2016. The protection of Tibetan antelopes has been widely expanded, and their population has increased to more than 150,000 (Yang et al. 2018). However, studies on their basic biological and behavioral information are limited because they occur at an extremely high elevation and in a harsh natural environment. Tibetan antelopes are usually sexually segregated but form mixed herds in the reproductive season in December and January. Tibetan antelopes can be divided into migratory and resident populations. Our focal population in Shenzha is a resident and does not migrate. The population size may reach 10,000 (Luo et al. 2018; Yang et al. 2018).

Tibetan gazelles are widely distributed on the Qinghai–Tibetan Plateau (Schaller 1998). Despite their wide distribution, their population has been decreasing in recent decades. Tibetan gazelles have been classified as a category II protected wild animal species in China and nearly threatened in the IUCN red list of threatened species (Zhang and Jiang 2006). Tibetan gazelles are much smaller than Tibetan antelopes, and they are both sexually segregated. Mixed herds are mainly found in the rutting season in December and January; afterward, they separate and aggregate in single-sex groups (Lian et al. 2004). Focal populations are estimated at a few hundred in Shenzha (Yang et al. 2018).

Behavioral observations.—Daytime observations were carried out from sunrise to sunset (Chinese standard time 0900–2000 h, equal to local time 0700–1800 h) in two summer periods (July and August in 2016; June and July in 2017). A group was defined as a herd of antelopes or gazelles with a distance of no more than 50 m between two group members (Luo et al. 2018; Yang et al. 2018). Samples were obtained by using a camcorder and binoculars in this study, and individuals were observed via the focal sampling method (Altmann 1974). Detailed information about focal groups and individuals, including species (Tibetan antelopes and gazelles), sex–age (adult male, subadult male, female), weather (sunny, cloudy, overcast, or rainy), and group size was recorded.

The encountered groups were randomly selected during our drive along the road. One focal subject from the selected group was randomly chosen, and a few more subjects were considered from different parts of the group if the group was large. The route was not repeated within three consecutive days to avoid duplicate sampling. The same individuals were unlikely to be sampled more than once on a given day because of the large size of the population, although the animals were not marked. Some individuals might have been sampled again,

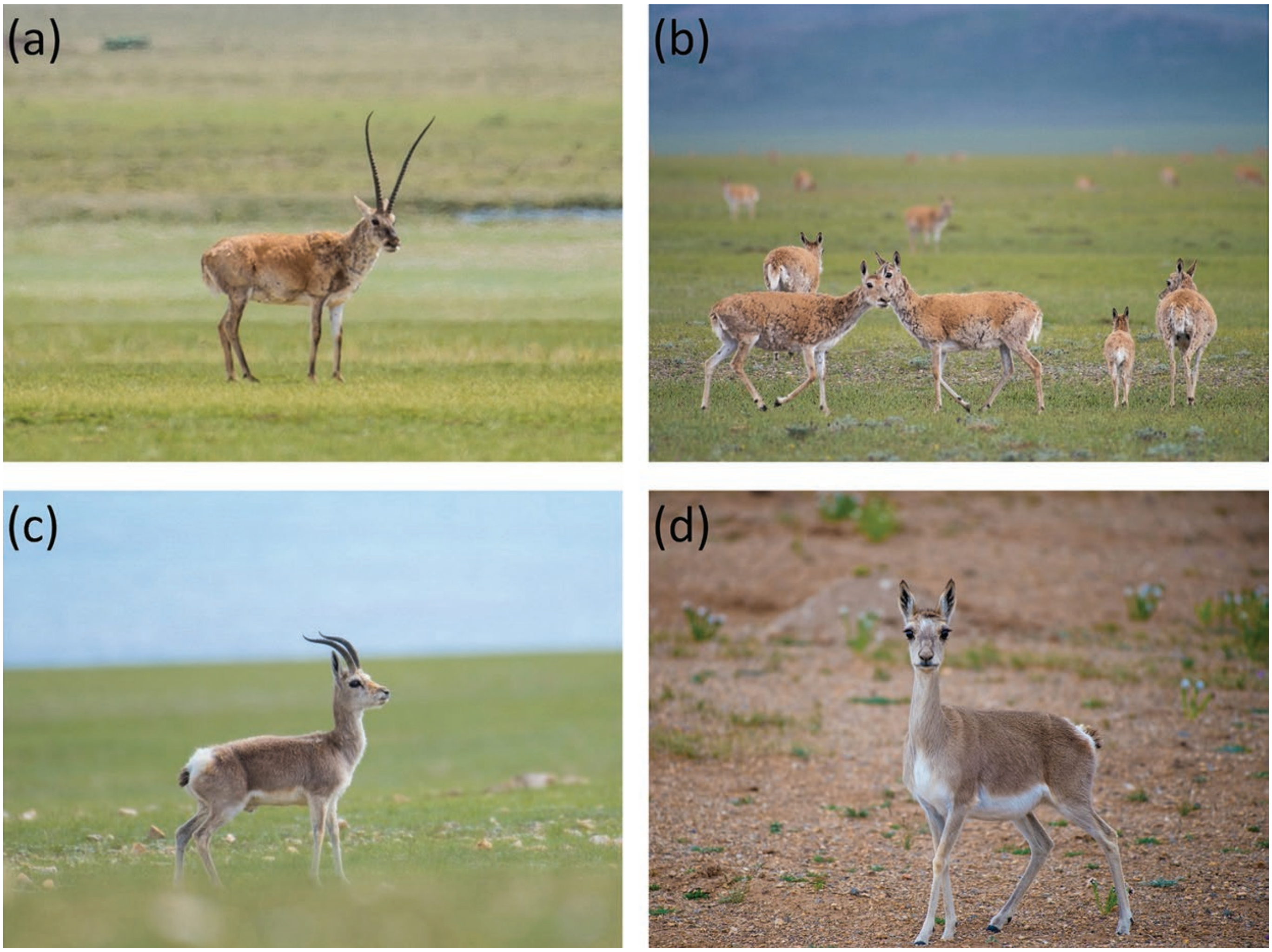

Fig. 1.—Photos of sympatric Tibetan antelopes (*Pantholops hodgsonii*; a—male, b—female and lamb) and Tibetan gazelles (*Procapra picticaudata*; c—male, d—female) by Yiqian Wu in Selincuo National Nature Reserve, Tibet in summer of 2017.

but the possibility was low. Each individual was considered an independent sample. Solitary individuals were also considered as a group with only one member.

Behavioral events were videotaped or dictated to a mobile phone recorder. Observations lasted 30 min unless the focal individual was lost in sight. The actual observation duration was 5–30 min. "Vigilance" behavior was defined as the upward stretching of the head of an ungulate while scanning around (Li 2016).

This study was an observational experiment, and observations were made at a distance of more than 200 m. All the experimental procedures in this study were approved by the Chinese Wildlife Management Authority.

Statistical analysis.—A total of 269 behavioral samples representing 4,066 min for Tibetan antelopes and 208 behavioral samples representing 3,540 min for Tibetan gazelles were collected. Two vigilance variables, namely, scan rate (number of vigilance scans per min) and proportion of time spent in vigilance (%), were calculated for each behavioral sample.

Scan rate was $\ln(X + 1)$ transformed, while the proportion of time in vigilance was $\arcsin\sqrt[4]{X}$ transformed to meet the requirements for the normal distribution. Then, a mixed linear model was set up to explore if vigilance was affected by species, sex–age, weather, and group size. Weather did not have a significant effect, so it was removed from the final model. In the final model, species, sex–age, and group size were entered as independent fixed factors and group ID was set as a random factor because some samples were collected from the same group. All the factors (species × sex–age, species × group size, and group ID) were, respectively, nested in the model. Then, the effect of group size on vigilance in male and female Tibetan antelopes was analyzed separately by using a similar mixed linear model (group size as an independent fixed factor, and group ID as a random factor). R language (R-3.5.1) with nlme package (Batary et al. 2012) was used for statistical analysis, and two-tailed probabilities of 0.05 were considered significant.

Results

The mixed linear model indicated that the vigilance of Tibetan gazelles was much higher than that of Tibetan antelopes (scan rate: $t = 5.207$, $P < 0.001$; Table 1; proportion of time in vigilance: $t = 3.514$, $P = 0.001$; Table 2). The median scan rate of Tibetan gazelles was 0.98 per min (ranging from 0.07 to 3.30), which was much higher than that of Tibetan antelopes at 0.26 per min (ranging from 0.00 to 1.93); similarly, the median proportion of time in vigilance by Tibetan gazelles was 18.52% (ranging from 0.57% to 100.00%). This value was approximately five times that of Tibetan antelopes, which spent only 3.79% of the time in vigilance (ranging from 0.00% to 76.95%; Fig. 2).

Sex–age had an opposite effect on the vigilance of the two ungulates. In Tibetan antelopes, the scan rate of the females was higher than that of the adult males ($t = -2.334$, $P = 0.020$; Table 1). In Tibetan gazelles, the scan rate (t = 2.586, $P = 0.010$) and the proportion of time in vigilance (t = 2.396, $P = 0.017$) of the females were lower than those of adult males (Tables 1 and 2).

Group size had no obvious effect on the vigilance of the two species, but some marked points were observed. The scan rate decreased as group size increased (Fig. 3), but the effect was insignificant (scan rate: $t = -1.584$, $P = 0.115$; Table 1; proportion of time in vigilance: $t = -0.295$, $P = 0.768$; Table 2). The vigilance of male Tibetan antelopes marginally decreased as group size increased (scan rate: $t = -1.809$, $P = 0.075$; proportion of time in vigilance: $t = -1.662$, $P = 0.101$; Table 3; Fig. 4). The effect of group size on the proportion of time in vigilance of female Tibetan antelope was U-shaped. The vigilance initially decreased (group size from 1 to 120) and then increased (group size from 120 to 400) ($Y = 1.08E - 6 * X^2 - 2.65E - 4 * X + 0.11$; Fig. 5).

Discussion

Body-size effect.—Body size is an important factor in shaping vigilance behavior (Brivio et al. 2014). In our study, body size significantly affected the vigilance of Tibetan gazelles and antelopes.

Interspecifically, Tibetan antelopes were less vigilant than Tibetan gazelles because the former are nearly three times larger than the latter; Tibetan antelopes also behaved less vigilantly

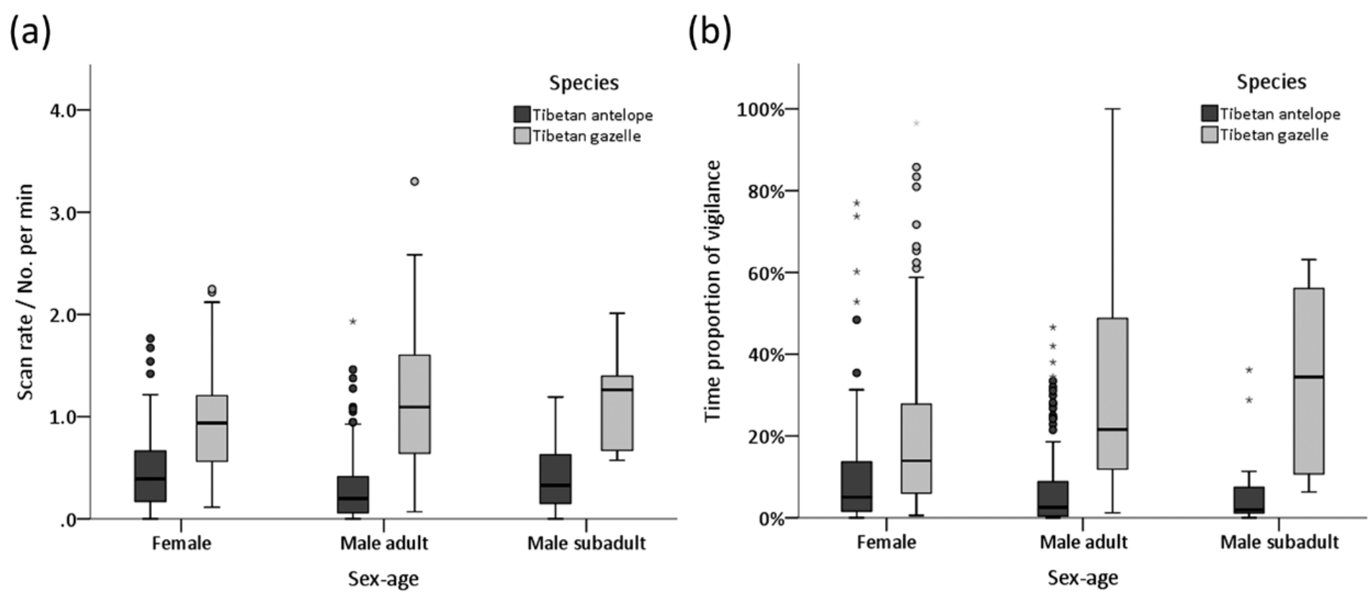

Fig. 2.—Inter- and intraspecific vigilance patterns of Tibetan antelopes (*Pantholops hodgsonii*) and Tibetan gazelles (*Procapra picticaudata*) in Selincuo National Nature Reserve, Tibet.

Table 1.—Effects of sex–age and group size on scan rate (number of scans per min) of sympatric Tibetan antelopes (*Pantholops hodgsonii*) and Tibetan gazelles (*Procapra picticaudata*) in Tibet with a mixed linear model. Significant relationships are indicated by bold *P*-values.

		Estimate	*SE*	*t*-value	*P*
Intercept		0.371	0.041	9.098	**<0.0001**
Species	Tibetan antelope	0			
	Tibetan gazelle	0.346	0.067	5.207	**<0.0001**
Tibetan antelope					
Sex–age	Female	0			
	Male-adult	−0.112	0.048	−2.334	**0.020**
	Male-subadult	−0.082	0.068	−1.198	0.232
Group size		−0.000	0.000	−0.292	0.771
Tibetan gazelle					
Sex–age	Female	0			
	Male-adult	0.174	0.067	2.586	**0.010**
	Male-subadult	0.180	0.114	1.584	0.114
Group size		−0.020	0.013	−1.584	0.115

Table 2.—Effects of sex–age and group size on proportion of time in vigilance by sympatric Tibetan antelopes (*Pantholops hodgsonii*) and Tibetan gazelles (*Procapra picticaudata*) in Tibet with a mixed linear model. Significant relationships are indicated by bold *P*-values.

		Estimate	*SE*	*t*-value	*P*
Intercept		0.460	0.033	14.088	**<0.0001**
Species	Tibetan antelope	0			
	Tibetan gazelle	0.188	0.053	3.514	**0.001**
Tibetan antelope					
Sex–age	Female	0			
	Male-adult	−0.059	0.039	−1.543	0.124
	Male-subadult	−0.074	0.056	−1.318	0.189
Group size		0.000	0.000	0.267	0.790
Tibetan gazelle					
Sex–age	Female	0			
	Male-adult	0.129	0.054	2.396	**0.017**
	Male-subadult	0.155	0.093	1.660	0.098
Group size		−0.003	0.010	−0.295	0.768

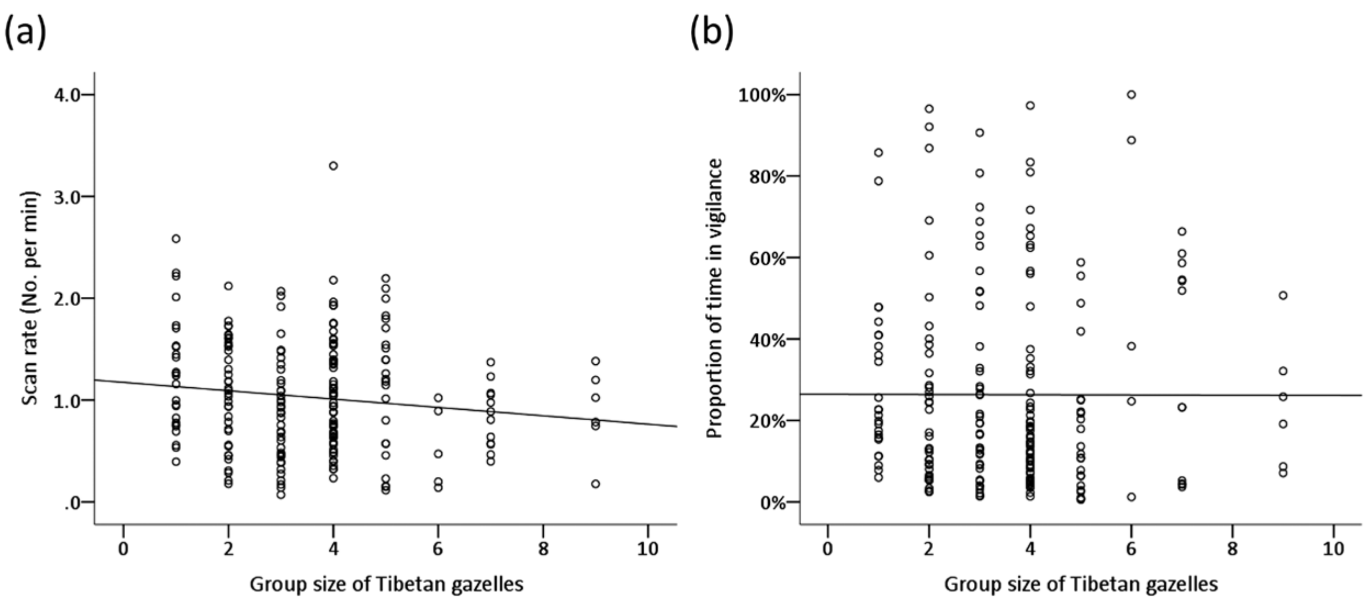

Fig. 3.—Group-size effects on vigilance (a—scan rate, b—proportion of time in vigilance) of Tibetan gazelles (*Procapra picticaudata*) in Selincuo National Nature Reserve, Tibet.

Table 3.—Effects of group size on vigilance of male Tibetan antelopes (*Pantholops hodgsonii*) with a mixed linear model. Significant relationships are indicated by bold *P*-values.

	Estimate	*SE*	*t*-value	*P*
Scan rate				
Intercept	0.314	0.037	8.583	**0.000**
Group size	−0.011	0.006	−1.809	0.075
Proportion of time in vigilance				
Intercept	0.447	0.036	12.270	**0.000**
Group size	−0.010	0.006	−1.662	0.101

probably because of their large group size. Thanks to the synergistic effect of group size and body size, Tibetan antelopes are much more tolerant to natural predators (Leslie and Schaller 2008; Leslie 2010). The average group size of Tibetan gazelles is less than five (Li and Jiang 2006). By comparison, the average group size of male Tibetan antelopes is almost twice that of Tibetan gazelles, and the average group size of female Tibetan antelopes is much higher than that of Tibetan gazelles. Thus, Tibetan antelopes living in large groups can benefit from their grouping advantage and are less vigilant. Similar results have been found in many other sympatric animals. For instance, following the reintroduction of wolves into Yellowstone National Park, elk (*Cervus elaphus*) significantly increased their vigilance, whereas larger bison (*Bison bison*) did not, and elk devoted more effort to vigilance than did bison (Laundre et al. 2001). Similar comparisons have been presented between Tibetan gazelles and Przewalski's gazelles (*P. przewalskii*) in the Upper Buha River Basin in the Qinghai–Tibet Plateau (Li 2016), and between sambar deer (*Rusa unicolor*) and takin (*Budorcas taxicolor*) in Wolong Nature Reserve in China (Liu et al. 2019).

Intraspecifically, body size affected the vigilance of Tibetan antelopes. The body mass of males is approximately 1.5 times that of females, making males much more resistant to predators than females (Cluttonbrock et al. 1982; Li et al. 2009). Predators are common in our study area; however, male Tibetan antelopes are not very sensitive to these predators and are even

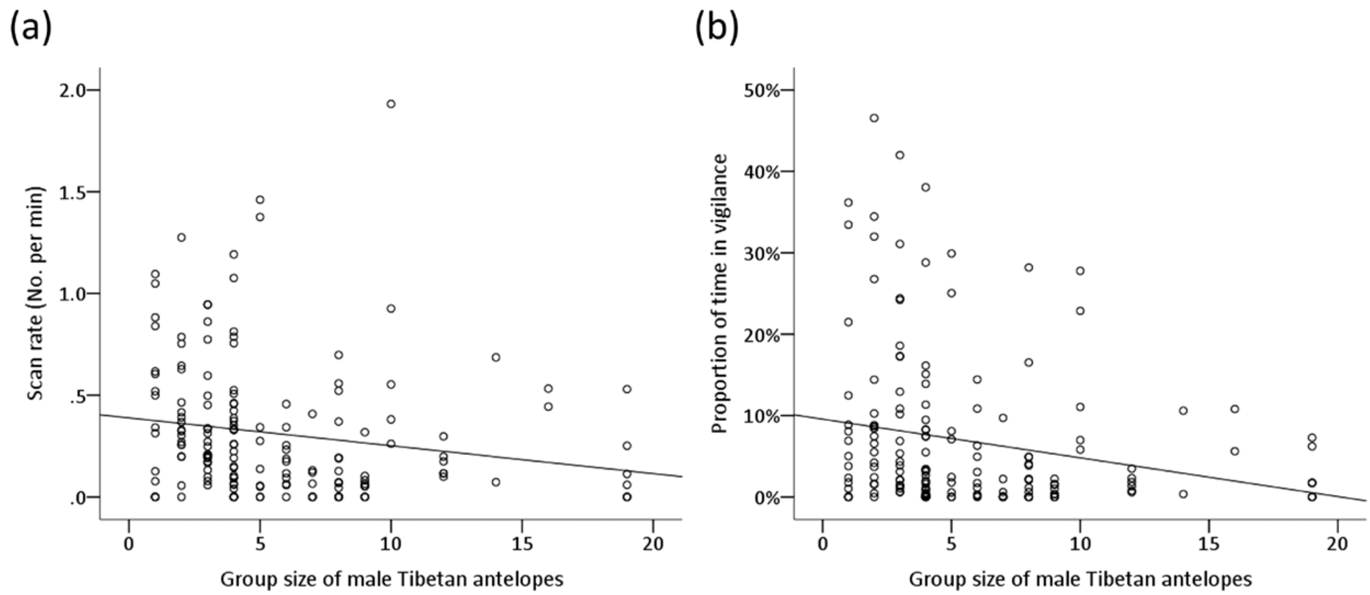

Fig. 4.—Group-size effects on vigilance (a—scan rate, b—proportion of time in vigilance) of male Tibetan antelopes (*Pantholops hodgsonii*) in Selincuo National Nature Reserve, Tibet.

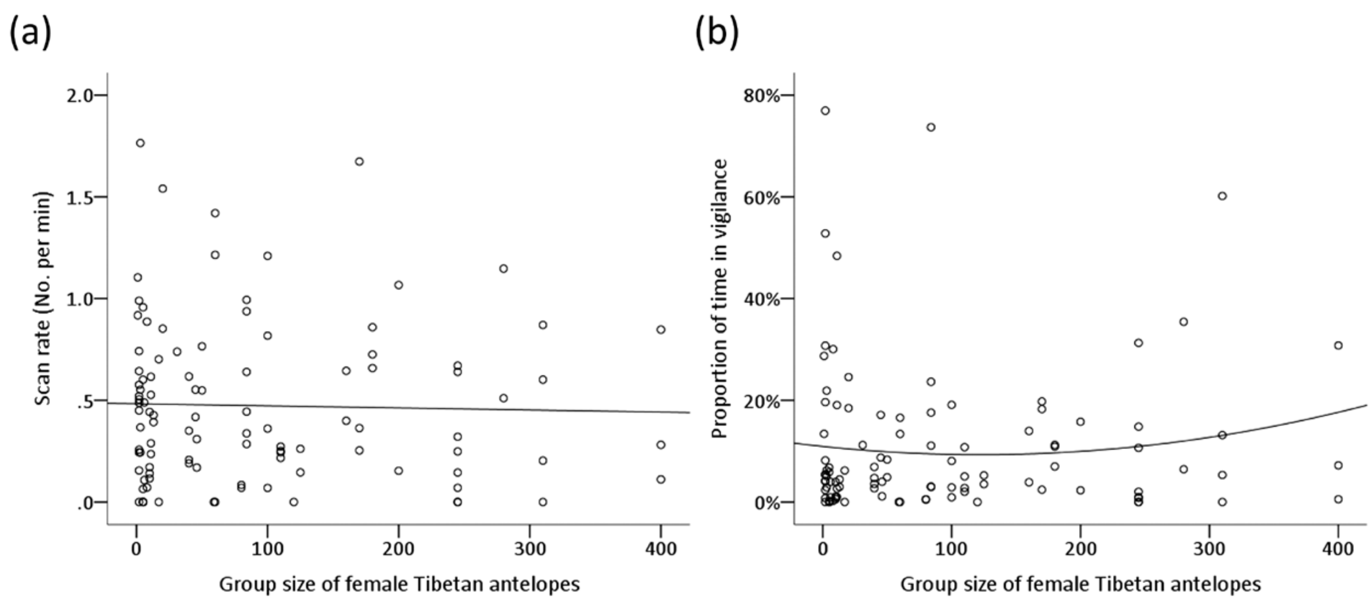

Fig. 5.—Group size effects on vigilance (a—scan rate, b—proportion of time in vigilance) of female Tibetan antelopes (*Pantholops hodgsonii*) in Selincuo National Nature Reserve, Tibet.

adopting a special puppet resting behavior in which they keep standing still for a certain time (Luo et al. 2018). In comparison with bedding resting behavior, individuals that are puppet resting are undoubtedly more easily found and targeted by predators. Hence, low vigilance and odd puppet resting among males are probably due to their much larger body size and better defensive ability against their natural enemies. This intraspecific body size effect also occurs in Père David's deer (*Elaphurus davidianus*—Zheng et al. 2013), elk (Childress and Lung 2003; Lung and Childress 2007), and merino sheep (*Ovis aries*—Michelena et al. 2006).

In Tibetan gazelles, we expected similar vigilance levels between males and females because both sexes have a similar body size (Leslie 2010). However, males were more vigilant than females, possibly because of the second function of vigilance as social monitoring (Li and Jiang 2008). Although our study period was not in the reproductive season, males were still competitive with one another, indicating that they had to remain vigilant to detect their potential competitors (Li and Jiang 2008). This social monitoring behavior increases the vigilance level of males in Tibetan gazelles, Przewalski's gazelles (Li et al. 2009), and impala (*Aepyceros melampus*—Shorrocks and Cokayne 2005).

Group-size effect.—Group size affects vigilance among many birds and mammals, such as red-crowned cranes (*Grus japonensis*—Wang 2011), black-necked cranes

(*G. nigricollis*—Xu et al. 2013; Yang et al. 2016), Przewalski's gazelles (Li et al. 2009, 2012; Shi et al. 2011), goitered gazelles (*Gazella subgutturosa*—Xia et al. 2011), Pere David's deer (Zheng et al. 2013), and springbok (*Antidorcas marsupialis*—Burger et al. 2000). However, this effect is not observed in some large mammals, such as giraffes (Cameron and Du Toit 2005), elk, and bison (Laundre et al. 2001), which have few natural enemies. A few studies have reported a negative effect of group size on the vigilance of Tibetan gazelles (Li and Jiang 2008) and Tibetan antelopes (Lian et al. 2007) outside our study area in Tibet. Thus, we expected a negative relationship between group size and vigilance in Tibetan gazelles and antelopes.

Vigilance of Tibetan gazelles decreased as group size increased, but the effect was not significant. This result was different from our previous study on Tibetan gazelles in the Upper Buha River Basin, Qinghai Province (Li and Jiang 2008). These two studies focused on different levels and employed different sampling methods. Our previous study in Qinghai was conducted at a group level, so we used a group scan sampling method. Conversely, our current study was performed at an individual level, so we applied a focal sampling method (Martin and Bateson 1986; Li and Jiang 2008). Hirschler et al. (2016) suggested that different methods may lead to different results. Moreover, the expression level of any group-size effect on vigilance may vary. For example, in black-necked cranes, this effect occurs at group and individual levels (Yang et al. 2016). By contrast, it may be observed only at a group level in Tibetan gazelles (Li and Jiang 2008).

Lian et al. (2007) reported a significant effect of group size on vigilance of Tibetan antelopes in Kekexili National Nature Reserve, but they focused on small groups of less than 30. For small groups, the proportion of time in vigilance decreased as group size increased. This observation was consistent with a previous study (Lian et al. 2007). However, for large groups, the proportion of time in vigilance increases as group size increases. Scramble competition and social monitoring occur unavoidably when groups become extremely large (Hall 1960). This social vigilance is different but difficult to distinguish from antipredator vigilance through field observation (Beauchamp 2016). Interference and competition from group members are obviously high in large groups, thus weakening the effect of group size (Beauchamp 2001; Blumstein et al. 2001). Females can form extremely large groups of more than a few hundred or even a few thousand in summer, and an interesting U-shaped vigilance pattern can be found. A similar U-shaped pattern has been found in large groups of red-crowned and common cranes (*G. grus*—Yang et al. 2006; Wang et al. 2011). The male groups were much smaller than the female groups, and the effect of group size on the vigilance of male Tibetan antelopes was marginally significant.

In conclusion, we found a significant effect of body size on the vigilance of Tibetan gazelles and antelopes at inter- and intraspecific levels. Group size did not affect the vigilance of Tibetan gazelles, but a marginal effect on the vigilance of male Tibetan antelopes was observed. Future studies may attempt to distinguish social vigilance from antipredator vigilance and make a comprehensive prediction of the effect of group size. Studies during the reproductive season will also enhance our understanding of vigilance mechanisms and functions.

Acknowledgments

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