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ORIGINAL PAPER

Influences of sex, group size, and spatial position on vigilance behavior of Przewalski's gazelles

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Abstract Group-living animals may need to spend less time being vigilant, consequently, having more time for other important activities such as foraging (i.e., group size effect). Przewalski's gazelle (*Procapra przewalskii*) is a group-living social animal, and a study was conducted in Qinghai Province of China during June–August 2006 by using a continuous focal sampling method to investigate the influences of group size, sex, within-group spatial position, and nearest-neighbor distance on individual vigilance level (defined as scanning frequency per minute). Male gazelles were more vigilant than females. The gazelle's vigilance level decreased with group size (group size effect), but only for females. The individuals at the central positions within a group were less vigilant than those at the peripheral positions, but the nearest-neighbor distance did not have any significant influence on the individual vigilance level. Our results support the hypotheses of group size effect and edge effects, but the sexual difference in vigilance level and in the response to group size effect on vigilance suggests that there may be sexual difference in the function and targets of vigilance behavior of Przewalski's gazelles, which warrants more investigation, with incorporation of within-group spatial position, to better understand the mechanism underlying the group size effect and edge effect.

Keywords Przewalski's gazelle · Vigilance behavior · Scanning frequency · Edge effect · Qinghai Lake

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Introduction

One of the most important benefits of group living is collective anti-predatory vigilance (Elgar 1989), and many previous studies have found vigilance to vary with predation risk, group size, sex, individual position within a group (central vs. peripheral), social status, and distance to the nearest neighbor (see reviews by Elgar 1989; Beauchamp 2003, 2008). Among all these factors, group size and sex may be the two that have received most attention in recent decades (Beauchamp 2008; Li et al. 2009).

Studies carried out across many different taxa have reported a negative correlation between group size and vigilance, i.e., individual animals commonly decrease their vigilance in larger groups (see Elgar 1989; Beauchamp 2003; Beauchamp 2008 for reviews). This inverse relationship between group size and individual vigilance level is often attributed to the anti-predator function of vigilance (see review by Elgar 1989). Central to this hypothesis is the "many eyes" effect (Pulliam 1973), which suggests that as group size increases in socially foraging animals, there are more eyes watching for predators and this increases the likelihood of their detection. Individuals can therefore devote more time to foraging without increasing their personal risk of being preyed upon (Lima 1995). In addition to the "many eyes" effect, individuals may decrease their investment in vigilance in larger groups due to decreased risk of predation caused by dilution (dilution effect, Quenette 1990) or greater confusion of a predator (if attack happens, Lima 1995; Roberts 1996). Such an inverse relationship is related to the benefits of group living in terms of greater probability of detecting a predator or a decrease in being predated. Therefore, if vigilance behavior reduces foraging time or efficiency and group size reduces an individual's need for vigilance behavior, vigilance level should decrease with an increase in group size.

Some studies have shown that individual vigilance levels differ between males and females, but there have been debates about which sex is more vigilant (Elgar 1989; Lian et al. 2007; Li and Jiang 2008). For example, Burger and Gochfield (1994) did not find any significant differences in vigilance between male and female impala (*Aepyceros melampus*) nor did Ebensperger et al. (2006) in degu (*Octodon degus*). Male Tibetan gazelles (*Procapra picticaudata*) have been reported to be more vigilant than females in Qinghai-Tibetan plateau (Li and Jiang 2008), and so have males in other ungulate species such as African buffalo (*Syncerus caffer*, Prins and Iason 1989) and springbok (*Antidorcas marsupialis*, Burger et al. 2000). Breeding status may confound the effect of sex on vigilance level, and some studies have shown that female ungulates with lambs are more vigilant than females without lambs (Childress and Lung 2003; Lian et al. 2007; Li et al. 2009).

In addition to group size and sex, some other factors also affect individual vigilance and confound group size effect on vigilance, among which nearest-neighbor distance and spatial position within a group are two important ones (Dias 2006; Di Blanco and Hirsch 2006; Fernández-Juricic et al. 2007; Blanchard et al. 2008; Fernández-Juricic and Beauchamp 2008). It has been shown that the vigilance behavior in the red-billed chough (*Pyrrhocorax pyrrhocorax*) depends more on neighbor distance than on group size (Rolando et al. 2001), but the direction of influence of neighbor distance on vigilance level is debatable. For example, a close proximity to group mates is associated with a lower vigilance rate in the teal (*Anas crecca*, Pöysä 1994), but it is predicted by Fernández-Juricic et al. (2007) that vigilance would be reduced as neighbor distance increased. More studies are thus needed, particularly on mammals in the field, to understand the effect of neighbor distance on vigilance behavior.

Some studies have investigated vigilance behavior with respect to within-group spatial position, although those are much fewer than studies on the effect of group size. Such studies have typically demonstrated that peripheral individuals are more vigilant than central individuals (Dias 2006; Di Blanco and Hirsch 2006; Blanchard et al. 2008). This edge effect is linked to the idea that peripheral individuals within a group undergo higher risks of predation due to fewer neighboring conspecifics, have higher "domains of danger," and thus, are more exposed to predation and tend to be more vigilant and to shift to the central positions (hypothesis of the selfish herd, Hamilton 1971). The geometry of a group is important in inducing a center–edge effect, but the presence of such an effect is also dependent on the place of origin of the predatory attack (Stankowich 2003). For example, an avian predator attacking a two-dimensional group from above may not produce the same center–edge effect that a terrestrial predator would. Despite the importance of within-group spatial position in determining vigilance level, this factor has typically not been incorporated in studies on vigilance behavior (Di Blanco and Hirsch 2006).

There have been many studies on animal vigilance level, but very few such studies have incorporated effects of group size, sex, group geometry, and nearest-neighbor distance in one study, particularly in the field. In this study, we aimed to investigate the effects of these four factors on the vigilance behavior of the Przewalski's gazelle in the Qinghai Lake area, China. The gazelles are group-living social animals and undergo high predation risk from a terrestrial predator—wolves (*Canis lupus*, Jiang 2004). We intended to determine: (1) whether individual vigilance level decreases with group size, (2) whether and how sex influences individual vigilance level, (3) whether and how the nearest-neighbor distance influences the individual vigilance level, and (4) whether and how the within-group spatial position influences the individual vigilance level.

Study area and animal population

This study was conducted in Hudong-Ketu area (99°50′–100°46′ E, 36°41′–37°55′ N), which is located to the south-east of Qinghai Lake in Qinghai Province. Hudong-Ketu area is one of the seven main distribution areas of the gazelle populations around Qinghai Lake (Jiang et al. 2001; Ye et al. 2006, Fig. 1). The altitude of this area ranges from 3,036 to 3,226 m. The average annual temperature is −0.7°C. The average minimum temperature occurs in January (−10.4–−4.7°C), whereas the average maximum temperature occurs in July (10.4–15.2°C, see Jiang 2004).

The Przewalski's gazelle is endemic to China and is found only around Qinghai lake area in Qinghai Province. Przewalski's gazelle lives in social groups (Lei et al. 2001; You and Jiang 2005), but adult males and females are sexually segregated for most of the year and usually only come together immediately before and during the breeding seasons (You 2005). Three group types (single-male groups, single-female groups, and mixed-sex groups) can be found during summer (Li and Jiang 2006), but it is not common to observe the mixed-sex groups during summer. Female groups, with or without kids, are observed most

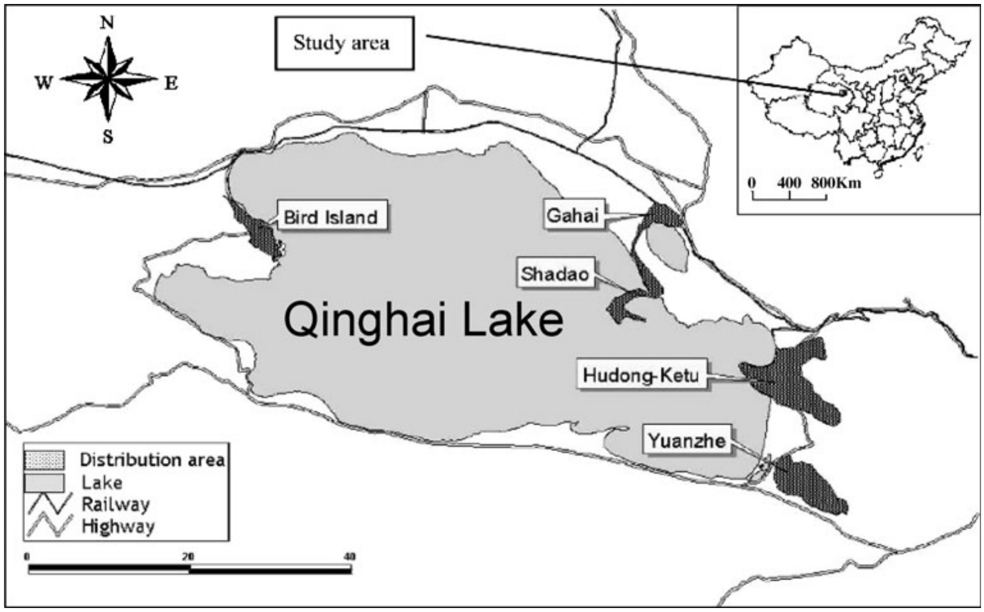

Fig. 1 Location of the study area around Qinghai Lake region in Qinghai Province [following Liu and Jiang (2004) with slight modification]

frequently. Przewalski's gazelle breeds from late December to early January and the lambing season is from late July to early August (You and Jiang 2005). The gazelle population in our study area consisted of ca. 120 unmarked free-ranging individuals.

Predation on gazelles in the study area was from wolves (Liu and Jiang 2003), and there was no predation from other terrestrial mammals or aerial predators. Although there have been no systematic and detailed studies on wolf density and predation rate in the study area, we recorded four observations in which gazelles were killed by wolves (personal observation, J. Shi). Local herdsmen also reported that the frequency of observing wolves increased much in recent years, and there were increasing cases of wolves killing their sheep.

Material and methods

Behavioral data collection

Przewalski's gazelles were considered to be vigilant when they interrupted feeding and raised their heads above shoulder height scanning their surroundings (Hunter and Skinner 1998). Vigilance level was therefore expressed as the scanning frequency per minute because the frequency of vigilance has been shown to be more sensitive to variation in group size than vigilance bout duration (e.g., Beauchamp 2008; Shi et al. 2010), and the scanning frequency is the pattern of vigilance, rather than simply the time allocated to vigilance that determines the probability of predator detection (Cresswell et al. 2003; Randler 2005).

Individual scanning frequency data were collected through continuous focal sampling methods (Altmann 1974; Shi et al. 2010) during June–August 2006. When a group of gazelles was found, animals were randomly chosen from the periphery and the center of the group. A group was defined as a herd of gazelles with the distance between any two group members being less than 50 m regardless of their behavioral state. Solitary individuals were considered groups of one, but such groups were excluded from analyses of effects of the nearest-neighbor distance. Individuals were considered as being positioned at the periphery if they were at the vertex of the smallest closed convex polygon enclosing all members of the group (Krause and Tegeder 1994) and in the center, if they were entirely enclosed by at least two layer of other group members (Rayor and Uetz 1990; see Stankowich 2003 for details).

Randomly chosen individuals were observed for 5 min during which records were made of the number of scanning events. Before the start of each observation, we recorded time, number of animals in the group, sex and age [only adults were sampled to avoid age effects on vigilance (Elgar 1989)] of the focal animals, location (periphery, or center), and the nearest-neighbor distance to the focal animal (using body length as an indication, Jiang 2004). A 5-min sample period was chosen because, at this time scale, changes of habitat, group size, and within-group spatial position rarely occurred. If any of them did occur, the sample was excluded from later analyses. Any observations that were less than 5 min were excluded from the final analyses.

All the observations were made through a telescope to count the number accurately. All observations were carried out during daylight between 0700 and 2000 hours, and we attempted to observe animals evenly over the daylight hours and to sample equally between both sexes. Female gazelles with lambs were excluded to avoid the influence of parental care on vigilance behavior (Childress and Lung 2003; Lian et al. 2007; Li et al. 2009). It was impossible to identify each individual gazelle in the field through its physical features, so it was likely that some individuals were sampled more than once during the study period. To minimize the risk of non-independent samples, the behavioral data were never recorded on more than two focal animals from the same group during the same day. Although a few individual animals might be sampled more than once during the whole study period, it is unlikely that observations of the same animals on different days in different environments and behavioral contexts were strongly autocorrelated (Molvar and Bowyer 1994).

Statistical analysis

Group size and scanning frequency were log-transformed to normalize their distributions (Shi et al. 2010). We used a general linear model to identify the effects of group size, sex, within-group spatial positions, and nearest-neighbor distance on individual vigilance level. The model included location (periphery vs. center), sex (male vs. female), group size, distance, and the interactions between these variables as fixed factors. The main effects of within-group spatial positions and sex on individual vigilance level were analyzed with Tukey's LSD method within the general linear model. If a significant effect of group size or nearest-neighbor distance was identified with the general linear model, we analyzed further their effects with Spearman's correlation method.

All analyses were conducted with SPSS 13.0 (Kinnear and Gray 2000). Differences were regarded as significant if $p<0.05$.

Results

A total of 196 focal observations were made to collect data on scanning frequency while the gazelle was feeding, among which 104 observations were on adult females and 92 were on adult males. The group size observed in this study ranged from 1 to 35 with an average of 8.7±4.3 (SD, a median of 9 individuals). There were 21 groups which had only one animal, accounting for about 11% of all groups, and they were excluded from the analyses of the nearest-neighbor distance effect.

The general linear modeling results indicated a significant effect of group size ($F_{32,42}=2.211$, $p=0.008$), within-group positions ($F_{1,42}=19.013$, $p<0.001$), and sex ($F_{1,42}=17.520$, $p<0.001$), but no significant effect of the nearest-neighbor distance ($F_{17,42}=1.096$, $p=0.389$, Table 1). There were no interactions between the variables, except the interaction between group size and the nearest-neighbor distance ($F_{36,42}=1.735$, $p=0.043$) with the group size effect being lower as distance increased (Table 1).

The average scanning frequency of males (0.85±0.49, $n=92$) was higher than that of females (0.49±0.35, $n=104$, $p<0.001$). Because there was significant difference in scanning frequency between the two sexes, we conducted the Spearman's correlation analyses of group size effect for males and females separately. The results indicated that the individual vigilance level of females decreased greatly with group size ($r=-0.287$, $p=0.002$, $n=104$), but that of males remained unaffected by group size ($r=-0.138$, $p=0.19$, $n=92$,Fig. 2).

Regarding the within-group spatial position, the average distance (m) between focal animals and their nearest neighbors was 11.6±3.3 m ($n=175$, group size ≥2 here). The scanning frequency of the peripheral individuals (0.74±0.48, $n=100$) was significantly higher than that of the central individuals (0.53±0.39, $n=96$, $p<0.001$).

Discussion

A statistically significant negative correlation between group size and individual vigilance level was observed in this study for Przewalski's gazelle, which is in accordance with many other previous studies in birds and mammals (e.g., Shorrocks and Cokayne 2005; Li and Jiang 2008; Li et al. 2009; also see reviews by Elgar 1989; Beauchamp 2008). If the hypotheses of many eyes effect and dilution effect are appropriate explanations of the group size effects, then our study may provide further evidence to support these hypotheses as the main driving force of ungulate social behavior (Elgar 1989; Beauchamp 2004).

Our results demonstrate that female gazelles showed the predicted negative relationship between group size and vigilance, and the vigilance level of male gazelles was higher than that of females. These sex biases in influence of group size on vigilance behavioral may reflect a corresponding difference in function and targets of vigilance behavior of Przewalski's gazelles. As suggested in other studies (e.g., Shorrocks and Cokayne 2005; Li and Jiang 2008), the female gazelles are probably scanning mainly for predators, and thus as group size increases, they can spend less time being vigilant and more time foraging. However, the male gazelles probably use their vigilance behavior for monitoring rival males, as well as for watching for females, in addition to watching for predators. Consequently, the males' vigilance is relatively independent of the number of individuals in the group, and thus, their vigilance level is not influenced by group size and is higher than that of females. It is not always easy and possible to distinguish the functions and targets of vigilance behavior in the field; however, our study suggests that more work is

Table 1 Results of general linear modeling analysis of effects of group size, sex, within-group position, and nearest-neighbor distance on the gazelle's individual vigilance level

Variables	Type III sum of squares	*df*	Mean square	*F*	Significance
Sex	2.090	1	2.090	17.520	0.000
Position	2.263	1	2.263	19.013	0.000
Distance	2.223	17	0.131	1.096	0.389
Log group size	8.439	32	0.264	2.221	0.008
Sex × position	0.161	1	0.161	1.352	0.251
Sex × distance	0.002	1	0.002	0.910	0.910
Position × distance	0.452	3	0.151	1.263	0.299
Sex × log group size	0.682	9	0.76	0.636	0.760
Position × log group size	3.040	15	0.203	1.699	0.089
Distance × log group size	7.450	36	0.207	1.735	0.043
Error	5.010	42	0.119		
Corrected model	34.855[a]	153	0.228	1.910	0.008
Intercept	17.983	1	17.983	150.753	0.000

[a] R^2 =0.874 (adjusted R^2 =0.417)

needed to investigate the sexual difference in function and targets of vigilance behavior to understand better the underlying mechanism of group size effects on vigilance in animals.

We observed no effect of nearest-neighbor distance on individual vigilance level, but a significant interaction between group size and the distance. Studies with other vertebrates (e.g., birds) have found that the strength of the group size effect varies with neighbor distance and is weakest when individuals are furthest away from each other (Fernández-Juricic et al. 2007), which is supported by our result for the gazelle. However, our result does not support the findings by Pöysä (1994) and Rolando et al. (2001) who stated that nearest-neighbor distance had a significant effect on vigilance in teals and red-billed chough, respectively. A nonlinear effect of neighbor distance on vigilance has also been noted in starlings (*Sturnus vulgaris*, Fernández-Juricic et al. 2004). It is predicted that, in birds, correlation between vigilance level and nearest-neighbor distance may no longer hold if individuals forage away from each other to such an extent that the effect is negated (Fernández-Juricic et al. 2007). Our result seems to support this prediction because the nearest-neighbor distance in the gazelle was averaged at 11.6±3.3 m, which was possibly far enough to prevent detection and dilution from operating, and thus, individual vigilance level was less affected by the nearest-neighbor distance.

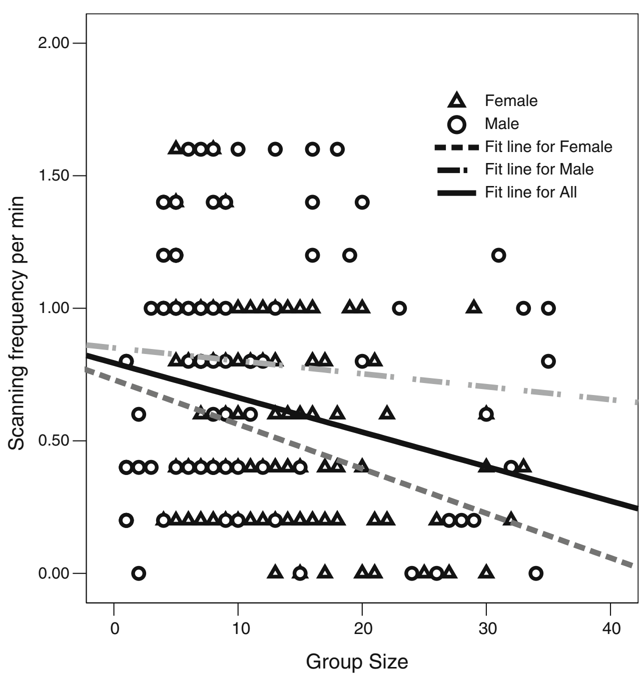

Fig. 2 There was a significant negative correlation between group size and vigilance rate of Przewalski's gazelles in Qinghai Lake (r=-0.277, p<0.001), showing sexual difference in responses to group size effects on vigilance

The results of this study support the prediction of "edge-effect" because individual gazelles at the periphery of a group were more vigilant than their central conspecifics and corroborate the findings of previous investigators whose data also support the prediction (e.g., Dias 2006; Blanchard et al. 2008). Although the lower vigilance level of central individuals may be because those individuals concentrate around a high-quality patch of slowly depleted food and increase their intake rate (Krause 1994; Hirsch 2007), this is less likely to happen in our study because the food resources were sparsely and evenly distributed across the study area (Liu and Jiang 2002). Due to the characteristics of food distribution and the neighbor distance in our study, the competition between individuals may remain at such a minimized level that the lower vigilance level of the central gazelles is unlikely a result of the difference in competition level between the central and peripheral positions of a group (Elgar 1989; Blumstein et al. 2001; Beauchamp and Ruxton 2003), but rather a result of difference in perception of predation risk.

Di Blanco and Hirsch (2006) have demonstrated that the spatial position with respect to group direction (e.g., front edge, end edge, etc.) is an important factor in determining individual vigilance level, but most of such studies (including our present one) have not measured the spatial positions with respect to the direction of the group (see Janson 1990; Black et al. 1992). Therefore, further studies on vigilance behavior should be carried out to integrate the effect of spatial position with respect to the group direction.

In summary, our study has demonstrated that individual vigilance level of the Przewalski's gazelle decreases with increasing group size in females, but not males. Male and female gazelles may use vigilance behavior for different functions although anti-predator behavior may be one of the major driving forces for the gazelle to maintain vigilance and aggregate together in Qinghai Lake area. Our study has also shown that within-group spatial position is an important factor to be taken into account in the study of vigilance behavior. However, further study is needed to investigate the possible sex-specific functions and targets of vigilance behavior and the effect of within-group spatial position with respect to the group direction in the field.

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