

Vigilance in Przewalski's gazelle: effects of sex, predation risk and group size

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Abstract

Vigilance in social animals is often aimed at detecting predators. Many social and environmental factors influence vigilance, including sex, predation risk and group size. During the summer of 2007, we studied Przewalski's gazelle *Procapra przewalskii*, an endemic ungulate to the Qinghai-Tibet Plateau, to test whether and how these three factors affect vigilance. We distinguished groups consisting of males, mothers with lambs and females without lambs making observations on groups in the presence or absence of nearby predators. We assessed the group-size effect on vigilance and how this varied with levels of predation risk and sex. Males and mothers scanned longer and with a higher frequency than females without lambs. Individuals were more vigilant under direct predation threat. Although vigilance generally decreased with group size, the extent of the decrease was independent of predation risk and was not significant in males. The results suggest that mothers are more vigilant suggesting greater vulnerability and that males may have increased their vigilance to compete for higher social ranks. The positive correlation between vigilance and predation risk and the negative correlation between vigilance and group size are consistent with earlier findings, but we failed to find an interaction between group size and predation risk on vigilance perhaps because vigilance levels are low even in small groups, thus making similar vigilant upward adjustments in both small and large groups.

Introduction

Vigilance behaviour in many animal species is often aimed at detecting predators (Krause & Ruxton, 2002). Changes in vigilance behaviour in this context have been linked to many social and environmental factors, including sex, predation risk and group size (Roberts, 1996). With respect to sex, several studies have documented sexual differences in vigilance levels, although which sex is more vigilant is not consistently the same (Elgar, 1989; Childress & Lung, 2003; Cameron & Du Toit, 2005). Vigilance in general can be aimed at conspecifics within the group or at predation threats from outside the group. In this context, differences in vigilance between the sexes have been related to sexual differences in foraging and breeding strategies (Ginnett & Demment, 1997; Reboresda & Fernandez, 1997). For example, in impala *Aepyceros melampus*, breeding males are more vigilant as they spend extra time searching for mates and monitoring rival males (Shorrocks & Cokayne, 2005), whereas in Rocky Mountain elk *Cervus elaphus*, females with calves are the most vigilant group members because calves are more vulnerable to predation (Childress & Lung, 2003).

Vigilance behaviour is also thought to reflect levels of predation risk (Hunter & Skinner, 1998; Laundre, Hernandez & Altendorf, 2001). For example, in Eastern grey kangaroos *Macropus giganteus*, individuals increased their scanning behaviour under high predation risk (Colagross & Cockburn, 1993). However, the relationship between vigilance and predation risk is not always consistent (Berger & Cunningham, 1988; Cameron & Du Toit, 2005). In giraffes *Giraffa camelopardalis* for instance, levels of vigilance are not adjusted according to perceived predation risk (Cameron & Du Toit, 2005). These discrepancies suggest that more detailed research is needed to explore whether and how predation risk affects vigilance.

A negative relationship between group size and vigilance, which is referred to as the 'group-size effect' on vigilance, has long been documented in many species of birds and mammals (Elgar, 1989; Roberts, 1996; Beauchamp, 1998). Three main hypotheses have been proposed to explain this negative relationship: the 'many-eyes' hypothesis or detection effect (Pulliam, 1973), the 'safety in numbers' hypothesis or dilution effect (Foster & Treherne, 1981) and the 'scramble competition' hypothesis (Clark & Mangel, 1986;

Beauchamp & Ruxton, 2003). The first two hypotheses emphasize the role of predation risk in shaping vigilance levels while the 'scramble competition' hypothesis highlights the need to adjust vigilance levels to increase the share of limited food resources. Regardless of the underlying mechanisms, the group-size effect on vigilance is lacking in several species including primate species (Treves, 2000), giraffes (Cameron & Du Toit, 2005) and Rocky Mountain elk (Laundre *et al.*, 2001). Therefore, more studies on the group-size effect on vigilance are needed to examine whether and how the effect takes place.

Interestingly, the strength of the group-size effect on vigilance may be dependent on the level of predation risk. Indeed, models predict that the decrease in vigilance with group size will be stronger when the risk of predation is lower (Manor & Saltz, 2003; Bohlin & Johnsson, 2004) implying there is an interaction between group size and predation risk. The reason behind this expectation is that low vigilance levels may be too costly to maintain even in large groups when the risk of predation is high. Evidence with respect to this prediction is mixed with support in some studies (Saino, 1994; Frid, 1997; Sadedin & Elgar, 1998; Lima, Zollner & Bednekoff, 1999; Burger, Safina & Gochfeld, 2000; Manor & Saltz, 2003) but not in others (Underwood, 1982; Hunter & Skinner, 1998; Harkin *et al.*, 2000; Childress & Lung, 2003; Monclús & Rödel, 2008).

Here, we use the Przewalski's gazelle *Procapra przewalskii*, an endemic ungulate to Qinghai-Tibet Plateau, as a study animal, to explore: (1) whether there is a difference in vigilance levels between males and females and in relation to the presence of lambs; (2) whether individuals increase vigilance under high predation risk; (3) whether vigilance decreases with increasing group size and finally (4) whether the group-size effect on vigilance is different with varying levels of predation risk and for different sexes. With respect to the last issue, gazelles forage in homogenous alpine meadows with a large supply of food thus limiting the role of food competition in driving vigilance levels. Indeed, interactions between group members are rarely related to food but rather to competition for mates (Walther, Mungall & Grau, 1983). We also assessed predation risk directly by measuring vigilance levels in the presence or absence of their main predators.

Methods

Study area and subjects

This study was conducted in the Upper Buha River Valley, Tianjun County, Qinghai Province, China (36°53'30"–48°39'12"N, 96°49'42"–99°41'48" E), located in the north-western part of the Qinghai Lake watershed area and south of the Qilian Mountains. Elevations range from 2850 to 5826 m above sea level with an average elevation of 3800 m. Local climate is characterized by dry, cold and long winters, strong winds, high levels of solar radiation and a short frost-free period. Mean annual temperature was -1.5°C with an extreme recorded low temperature of -40°C . Annual pre-

cipitation varies from 330 to 412 mm and most rain falls between June and September. Alpine meadow is the main vegetation type in the study area. Shrubs are found along the Buha River Valley, which is the largest river flowing into the Qinghai Lake.

The Przewalski's gazelle only occurs around Qinghai Lake and total population size was estimated to be <300 individuals in 1990s (Jiang *et al.*, 1995; Jiang, Feng & Wang, 1996; Jiang, Li & Wang, 2000). After 20 years of protection, there are still only several hundred gazelles (Jiang, 2004; Li, Jiang & Li, 2008). It has been classified as Critically Endangered by the Species Survival Commission of the World Conservation Union-IUCN since 1996 and is a Category I (Endangered in China) National Protected Wild Animal Species in China since 1989. Przewalski's gazelle breeds from late December to early January and the lambing season is from late July to early August (You & Jiang, 2005; Li & Jiang, 2006). The focal population at the south of Buha River consists of about 100 unmarked individuals. The main predator is the wolf *Canis lupus*, with about 10 individuals in this area. Tibetan fox *Vulpes ferrilata*, are also common and may prey upon lambs of Przewalski's gazelle.

Behavioral sampling

Daytime observations were carried out by one of us (Z. L.) from sunrise to sunset between June and August 2007. We defined a group as a herd of gazelles with no more than 50 m separating any two group members. Observations were carried out from the roadside using binoculars (8 × 42) or a telescope (20–60 × 63). Distance of the focal group from the road was measured using a range finder and classified into one of three categories: < 100 m, between 100 and 300 m and > 300 m. We chose two different locations for observations and alternated observations between locations.

It was not practically feasible to mark individuals or to recognize individuals through particular features. Therefore, upon encountering a group, we randomly selected one but never more than two focal individuals per group. Because of the random selection process, focal individuals could occur anywhere in the group in terms of spatial location (edge or centre). As individuals are unmarked and population size is rather small, it is likely that the same individuals were monitored more than once during the study period. By focusing on at most two individuals per group, we reduced the chances of sampling the same individuals twice on the same day.

At the beginning of each focal observation, we recorded the date, time of day, location, distance to road, group size (individuals excluding lambs), the number of lambs present and level of predation risk. Only three stable group types (single-male groups, single-female groups and mother-lamb groups) could be found during summer (Li & Jiang, 2006). Focal gazelles were classified into three social categories: female with a lamb (mother), female without a lamb (female) or male (male). It was not practically feasible to distinguish adults from sub-adults and the two age classes were therefore collapsed. Predation risk was considered high

when predators (wolves or foxes) occurred within 300 m of the observed group, and low when no predators could be detected within 300 m. Wolves on the plateau rarely initiated attacks beyond 300 m of a focal group.

Behavioural events were dictated on to a MP3 recorder. Observations lasted 30 min unless we lost sight of the focal individual. Actual observation times ranged from 2 to 30 min, with an average of 19 min. We distinguished five behavioural states: feeding and searching (referred to as 'feeding'), bedding and ruminating ('bedding'), moving, vigilance and other behaviours. Feeding occurred when a gazelle grazed on the pasture or moved during a grazing bout with its head held below the horizontal plane. Bedding referred to sitting on the ground for rest and rumination. Moving consisted of a gazelle walking or running with its head held above the horizontal plane. Vigilance took place when a gazelle was standing up and scanning its surroundings, which could occur while moving or not. Other behaviours included grooming, fighting, defecating, lactating and nursing a lamb.

Scanning behaviour was used as our estimate of vigilance because (1) the head-up posture brings all the sensory organs to a position that should increase the detection range and (2) it is the observed state of alertness when a predator is detected (Childress & Lung, 2003).

Data analysis

From the timed sequences of events, time spent scanning was summed across the focal observation and expressed as a percentage of total observation time. Scan frequency represented the number of scans per min of observation and average scan duration was obtained by dividing time spent vigilant by the number of scans over the total focal observation duration. For the purposes of analysis, we used the arcsine square-root transformation for percentages of time spent scanning and the \log_{10} transformation for group size and average scan duration.

For the analysis of time spent scanning and average scan duration, we used a linear model including, location (two levels), distance to road (three levels), sex class (three levels), predation risk (two levels), group size (continuous factor), the interaction between group size and level of predation risk and the interaction between group size and sex class as fixed factors. *Post hoc* testing was carried out with Tukey's test.

For the analysis of scan frequency, we used a negative binomial regression model with the same fixed factors. The distribution of the number of scans per focal observation was highly skewed to the right with a variance much larger than the mean precluding the use of a Poisson model. The natural logarithm of total observation time was used as an offset in the model to control for different durations across focal observations. The fit of the negative binomial model, as assessed with the deviance, was good. *Post hoc* tests relied on contrasts between levels of the independent variable with a Bonferroni's correction for *P*-levels.

Two independent variables could only be examined in subsets of the data. The effect of season (classified as before

or after the beginning of the lambing season) was examined using the female and male categories only because these individuals are not involved in parental care which might influence time budgets. We failed to document any significant effect of season for any of the dependent variables ($P > 0.25$). Season was therefore ignored in subsequent analyses. In addition to group size, the number of lambs in the group might influence vigilance. For this analysis, we only considered mothers and using the same models described earlier we failed to document any effect of this variable for any of the dependent variables ($P > 0.14$). Proportion of lambs was therefore excluded from the following analyses.

Statistical analyses were carried out with SAS version 9.1 (Cary, NC, USA). The level of statistical significance was set at 0.05 throughout. We report mean and standard errors obtained from the statistical models and β parameters for group size.

Results

We collected 175 sets of focal observations representing 3384 min of observations. High predation risk occurred during 16 focal observations (9.1%). Level of predation risk was independent of sex class ($\chi^2_2 = 4.7$, $P = 0.14$). The nearest-neighbour distance in the gazelle groups was usually stable, ranging from 3 to 5 m. Observed groups ranged in size from one to 25 individuals although most observations included < 10 individuals.

The percentage time spent scanning was on average 5.4% and ranged from 0 to 40.9% (Fig. 1a). Location, distance to road and the interaction between level of predation risk and group size were non-significant and were removed from the model. The final model indicated a significant effect of sex class ($F_{2,168} = 16.9$, $P < 0.0001$), predation risk ($F_{1,168} = 16.3$, $P = 0.0003$), group size ($F_{1,168} = 7.7$, $P = 0.007$) and a significant interaction between group size and sex class ($F_{2,168} = 8.8$, $P = 0.0002$). Percentage time spent scanning decreased with group size in females ($\beta = -0.10 \pm 0.03$, $P = 0.006$) and in mothers ($\beta = -0.23 \pm 0.04$, $P < 0.0001$) but not in males ($\beta = 0.09 \pm 0.07$, $P = 0.19$). Percentage time spent scanning was higher when the level of predation risk was high (0.34 ± 0.03 , mean \pm SE) rather than low (0.21 ± 0.01). *Post hoc* tests indicated that time spent scanning was significantly lower in females (0.20 ± 0.02) than in mothers (0.33 ± 0.02) and in males (0.30 ± 0.03) but there was no difference between males and mothers.

Average scan duration was 8.4 s and ranged from 0 to 61.7 s (Fig. 1b). Location, distance to road and the interaction between level of predation risk and group size were non-significant and were removed from the model. The final model indicated a significant effect of sex class ($F_{2,168} = 6.9$, $P = 0.001$) and predation risk ($F_{1,168} = 8.5$, $P = 0.004$) but no overall effect of group size ($F_{1,168} = 1.1$, $P = 0.29$). There was a significant interaction between group size and sex class ($F_{2,168} = 5.1$, $P = 0.007$). Average scan duration decreased with group size in mothers ($\beta = -0.43 \pm 0.13$, $P = 0.001$) and more marginally in females ($\beta = -0.21 \pm 0.11$, $P = 0.06$) but

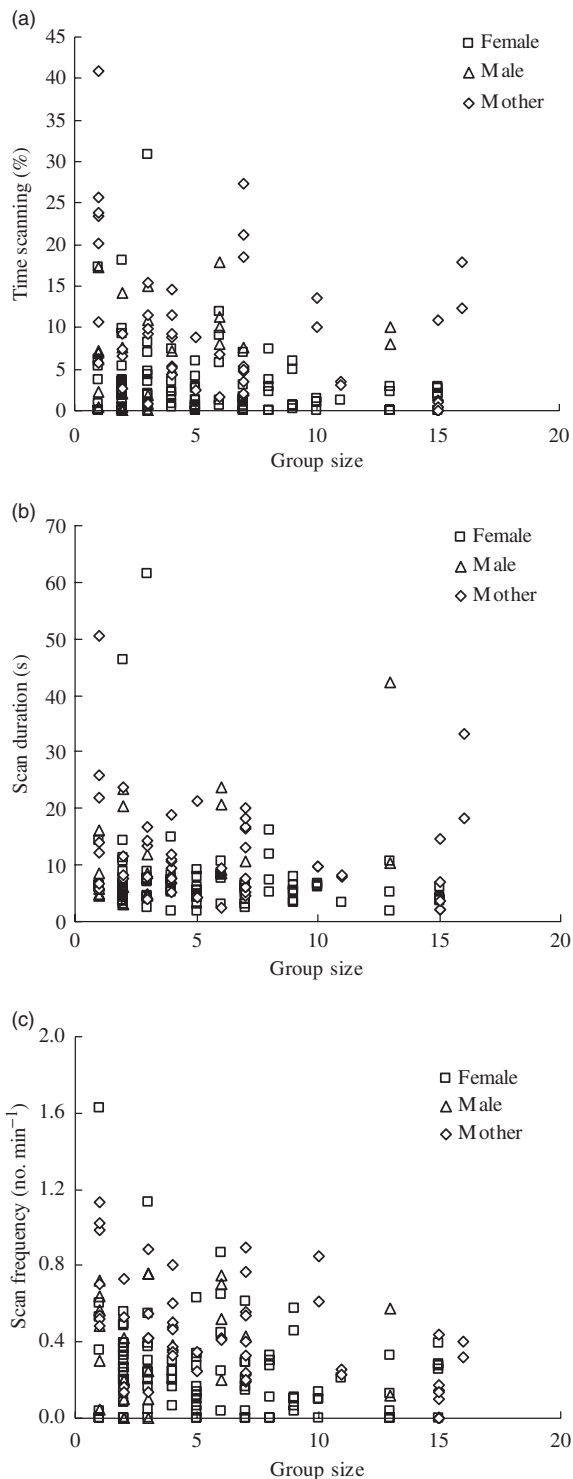


Figure 1 Time spent scanning (a), average scan duration (b) and scan frequency (c) as a function of group size and sex in Przewalski's gazelle *Procapra przewalskii* (squares: female; triangles: male; diamond: mother).

did not vary with group size in males ($\beta = 0.35 \pm 0.21$, $P = 0.10$). Average scan duration was higher when the level of predation risk was high (13.13 ± 2.08 s) rather than low (7.97 ± 0.69 s). *Post hoc* tests indicated that average scan duration was significantly lower in females (6.28 ± 0.79 s) than in mothers (11.57 ± 1.27 s) and in males (10.50 ± 1.82 s) but there was no difference between males and mothers.

Average scan frequency per min was 0.32 and ranged from 0 to 1.6 (Fig. 1c). Location, distance to road, the interaction between level of predation risk and group size and the interaction between group size and sex class were non-significant and were removed from the model. The final model indicated a significant effect of sex class ($\chi^2_2 = 13.5$, $P = 0.001$), predation risk ($\chi^2_1 = 6.3$, $P = 0.01$) and group size ($\chi^2_1 = 17.2$, $P < 0.0001$). The frequency of scanning decreased by a factor of 0.43 ± 0.09 or 57% for each unit of group size and increased by a factor of 1.82 ± 0.44 or 82% when predation risk was high rather than low. The frequency of scanning increased by a factor of 1.76 ± 0.27 or 76% in mothers when compared to females ($P = 0.0002$) but was not different between males and females ($P = 0.13$) or between males and mothers ($P = 0.23$).

Discussion

Several studies have shown that sex is an important correlate of individual vigilance levels (Childress & Lung, 2003; Cameron & Du Toit, 2005; Shorrock & Cokayne, 2005; Michelena *et al.*, 2006; Li & Jiang, 2008a; Monclús & Rödel, 2008). We found that mothers with lambs were the most vigilant among the three sex classes, although the difference between mothers and males was not significant. Mothers and males performed longer scans, at a higher frequency and thus spent more time scanning. Mothers with lambs are usually considered the most vulnerable because lambs are less able to detect and escape from predators (Clutton-Brock *et al.*, 1982). Therefore, mothers spend extra time scanning for predators so as to detect enemies earlier to escape or hide. This finding was also documented in Rocky Mountain elk (Childress & Lung, 2003).

Males were generally as vigilant as mothers and more vigilant than females without lambs. Some studies indicate that males are often less vigilant than females because they are larger and stronger and therefore can escape or withstand enemies more easily (Clutton-Brock *et al.*, 1982). Although there is support for this expectation in some species (Childress & Lung, 2003; Cameron & Du Toit, 2005; Michelena *et al.*, 2006), we failed to find similar results with gazelles. Other works suggest that males spend more time vigilant than females as they have to monitor the behaviour of other males and potential mates (Shorrock & Cokayne, 2005; Kutsukake, 2007; Li & Jiang, 2008a,b). Our results suggest that the targets of vigilance may be different between the sexes of Przewalski's gazelle.

With respect to predation risk, we found that individuals increased scan duration and the frequency of scanning when threatened directly by potential predators. Such an increase in vigilance may allow gazelles to evaluate the risk posed by

these predators more accurately. Higher vigilance levels when faced with direct predation threats have also been documented in other species (Caraco, Martindale & Pulliam, 1980; Glück, 1987; Saino, 1994). When predators appear near a group, there is no doubt that individuals benefit from higher vigilance. More vigilant foragers would detect or escape from predators earlier and shift the burden of predation to their less vigilant companions (FitzGibbon, 1989; Lima & Bednekoff, 1999; Cresswell *et al.*, 2003). This effect has been referred to as the 'pass-along effect' (Beauchamp, 2007).

In ungulates, the correlation between group size and vigilance has been reported to be negative, positive or absent (Elgar, 1989; Quenette, 1990). This variation may reflect the unique set of costs and benefits derived by each member from the presence of companions (Beauchamp, 2001; Childress & Lung, 2003). In recent studies, the relationship is still inconsistent. For instance, in kob antelope *Kobus kob kob*, vigilance decreased with group size (Fischer & Linsenmair, 2007), whereas in giraffes, group size had little effect on scanning behaviour in either males or females (Cameron & Du Toit, 2005).

We found a significant negative correlation between group size and vigilance in females and mothers, but not males of Przewalski's gazelle. Although scramble competition can play an important role in the group-size effect on vigilance (Beauchamp, 2003; Beauchamp & Ruxton, 2003; Randler, 2005a,b), we are confident that other factors underlie changes in vigilance in the Przewalski's gazelle. This is because scramble-competition effects are expected when foragers must jostle to obtain a greater share of limited resources (Beauchamp & Ruxton, 2003). However, gazelles in the study area graze on homogeneous alpine meadows and food resources are plentiful during summer for herbivores. Generally, predation pressure is considered the main driving force for the group-size effect on vigilance. Living in groups for gazelles is probably beneficial for each group member because of increased detection ability of predators and/or dilution of predation risk caused by wolves and foxes. However, the interaction between group size and sex suggests that additional factors should be considered. Variation in the strength of the group-size effect as a function of sex or social status has been documented in other species (Yaber & Herrera, 1994; Childress & Lung, 2003; Shorrocks & Cokayne, 2005). These studies suggest that vigilance aimed at rivals or mates may increase with group size in males mitigating any gains from reduced predation risk in large groups. Future work could establish the targets of vigilance in male gazelles to test this hypothesis further.

We did not find an interaction between group size and predation risk. Our finding is surprising because we can rule out food competition effects as a confounding factor and because we assessed predation risk quite directly. Obviously, small sample size, especially when gazelles are under direct predation threat, will reduce the power to detect a significant interaction. However, we note that vigilance levels are low even in small groups (5.4% time spent scanning on average in Przewalski's gazelle compared with 16.95% in impala,

Shorrocks & Cokayne, 2005), so that small groups can respond to an elevated predation risk by increasing vigilance levels just as well as large groups thus reducing the scope for an interaction between group size and predation risk. As pointed out earlier, there is no consensus on the strength of the interaction between group size and predation risk and we encourage more work on this topic.

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References

- Beauchamp, G. (1998). The effect of group size on mean food intake rate in birds. *Biol. Rev.* **73**, 449–472.
- Beauchamp, G. (2001). Should vigilance always decrease with group size? *Behav. Ecol. Sociobiol.* **51**, 47–52.
- Beauchamp, G. (2003). Group-size effects on vigilance: a search for mechanisms. *Behav. Processes.* **63**, 111–121.
- Beauchamp, G. (2007). Vigilance in a selfish herd. *Anim. Behav.* **73**, 445–451.
- Beauchamp, G. & Ruxton, G.D. (2003). Changes in vigilance with group size under scramble competition. *Am. Nat.* **161**, 672–675.
- Berger, J. & Cunningham, C. (1988). Size-related effects on search times in North American grassland female ungulates. *Ecology* **69**, 177–183.
- Bohlin, T. & Johnsson, J.I. (2004). A model on foraging activity and group size: can the relative importance of predation risk dilution and competition be evaluated experimentally? *Anim. Behav.* **68**, 1–5.
- Burger, J., Safina, C. & Gochfeld, M. (2000). Factors affecting vigilance in springbok: importance of vegetative cover, location in herd, and herd size. *Acta Ethol.* **2**, 97–104.
- Cameron, E.Z. & Du Toit, J.T. (2005). Social influences on vigilance behaviour in giraffes, *Giraffa camelopardalis*. *Anim. Behav.* **69**, 1337–1344.
- Caraco, T., Martindale, S. & Pulliam, H.R. (1980). Avian flocking in the presence of a predator. *Nature* **285**, 400–401.
- Childress, M.J. & Lung, M.A. (2003). Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? *Anim. Behav.* **66**, 389–398.
- Clark, C.W. & Mangel, M. (1986). The evolutionary advantages of group foraging. *Theor. Popul. Biol.* **30**, 45–75.
- Clutton-Brock, T.H., Iason, G.R., Albon, S.D. & Guinness, F.E. (1982). The effects of lactation on feeding behaviour

- and habitat use of wild red deer hinds. *J. Zool. (Lond.)* **198**, 227–236.
- Colagross, A.M.L. & Cockburn, A. (1993). Vigilance and grouping in the Eastern Gray Kangaroo, *Macropus Giganteus*. *Aust. J. Zool.* **41**, 325–334.
- Cresswell, W., Lind, J., Kaby, U., Quinn, J.L. & Jakobsson, S. (2003). Does an opportunistic predator preferentially attack nonvigilant prey? *Anim. Behav.* **66**, 643–648.
- Elgar, M.A. (1989). Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev. Camb. Philos. Soc.* **64**, 13–33.
- Fischer, F. & Linsenmair, K.E. (2007). Changing social organization in an ungulate population subject to poaching and predation – the kob antelope (*Kobus kob kob*) in the Comoe National Park, Cote d'Ivoire. *Afr. J. Ecol.* **45**, 285–292.
- FitzGibbon, C.D. (1989). A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. *Anim. Behav.* **37**, 508–510.
- Foster, W.A. & Treherne, J.E. (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature* **293**, 466–467.
- Frid, A. (1997). Vigilance by female Dall's sheep: interactions between predation risk factors. *Anim. Behav.* **53**, 799–808.
- Ginnett, T.F. & Demment, M.W. (1997). Sex differences in giraffe foraging behavior at two spatial scales. *Oecologia* **110**, 291–300.
- Glück, E. (1987). An experimental study of feeding, vigilance and predator avoidance in a single bird. *Oecologia* **71**, 268–272.
- Harkin, E.L., van Dongen, W.F.D., Herberstein, M.E. & Elgar, M.A. (2000). The influence of visual obstructions on the vigilance and escape behaviour of house sparrows, *Passer domesticus*. *Aust. J. Zool.* **48**, 259–263.
- Hunter, L.T.B. & Skinner, J.D. (1998). Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour* **135**, 195–211.
- Jiang, Z. (2004). *Przewalski's gazelle*. Beijing: Chinese Forestry Press.
- Jiang, Z., Feng, Z. & Wang, Z. (1996). Przewalski's gazelle in China. *Conserv. Biol.* **10**, 324–325.
- Jiang, Z., Feng, Z., Wang, Z., Chen, L., Cai, P. & Li, Y. (1995). Historical and current distributions of Przewalski's gazelles. *Acta Theriol. Sinica* **15**, 241–245.
- Jiang, Z., Li, D. & Wang, Z. (2000). Population declines of Przewalski's gazelle around Qinghai Lake, China. *Oryx* **34**, 129–135.
- Krause, J. & Ruxton, G.D. (2002). *Living in groups*. New York: Oxford University Press.
- Kutsukake, N. (2007). Conspecific influences on vigilance behavior in wild chimpanzees. *Int. J. Primatol.* **28**, 907–918.
- Laundre, J.W., Hernandez, L. & Altendorf, K.B. (2001). Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. *Can. J. Zool.* **79**, 1401–1409.
- Li, Z. & Jiang, Z. (2006). Group patterns of sympatric Przewalski's gazelle and Tibetan gazelle during the green grass period in Upper Buha River, Tianjun County, Qinghai Province. *Zool. Res.* **27**, 396–402.
- Li, Z. & Jiang, Z. (2008a). Group size effect on vigilance: evidence from Tibetan gazelle in Upper Buha River, Qinghai-Tibet Plateau. *Behav. Process.* **78**, 25–28.
- Li, Z. & Jiang, Z. (2008b). Sexual segregation in Tibetan gazelle: a test on the activity budget hypothesis. *J. Zool. (Lond.)* **274**, 327–331.
- Li, Z., Jiang, Z. & Li, C. (2008). Dietary overlap of Przewalski's gazelle, Tibetan gazelle and Tibetan sheep on the Qinghai-Tibet Plateau. *J. Wildl. Mgmt.* **72**, 944–948.
- Lima, S.L. & Bednekoff, P.A. (1999). Back to the basics of antipredatory vigilance: can nonvigilant animals detect attack? *Anim. Behav.* **58**, 537–543.
- Lima, S.L., Zollner, P.A. & Bednekoff, P.A. (1999). Predation, scramble competition, and the vigilance group size effect in dark-eyed juncos (*Junco hyemalis*). *Behav. Ecol. Sociobiol.* **46**, 110–116.
- Manor, R. & Saltz, D. (2003). Impact of human nuisance disturbance on vigilance and group size of a social ungulate. *Ecol. Appl.* **13**, 1830–1834.
- Michelena, P., Noël, S., Gautrais, J., Gerard, J.F., Deneubourg, J.L. & Bon, R. (2006). Sexual dimorphism, activity budget and synchrony in groups of sheep. *Oecologia* **148**, 170–180.
- Monclús, R. & Rödel, H.G. (2008). Different forms of vigilance in response to the presence of predators and conspecifics in a group-living mammal, the European rabbit. *Ethology* **114**, 287–297.
- Pulliam, H.R. (1973). On the advantages of flocking. *J. Theor. Biol.* **38**, 419–422.
- Quenette, P.Y. (1990). Functions of vigilance behavior in mammals – a review. *Acta Oecol.* **11**, 801–818.
- Randler, C. (2005a). Coots *Fulica atra* reduce their vigilance under increased competition. *Behav. Process.* **68**, 173–178.
- Randler, C. (2005b). Vigilance during preening in coots *Fulica atra*. *Ethology* **111**, 169–178.
- Reboreda, J.C. & Fernandez, G.J. (1997). Sexual, seasonal and group size differences in the allocation of time between vigilance and feeding in the greater rhea, *Rhea americana*. *Ethology* **103**, 198–207.
- Roberts, G. (1996). Why individual vigilance declines as group size increases. *Anim. Behav.* **51**, 1077–1086.
- Sadedin, S.R. & Elgar, M.A. (1998). The influence of flock size and geometry on the scanning behaviour of spotted turtle doves, *Streptopelia chinensis*. *Aust. J. Ecol.* **23**, 177–180.
- Saino, N. (1994). Time budget variation in relation to flock size in Carrion crows, *Corvus corone*. *Anim. Behav.* **47**, 1189–1196.
- Shorrocks, B. & Cokayne, A. (2005). Vigilance and group size in impala (*Aepyceros melampus* Lichtenstein): a study in Nairobi National Park, Kenya. *Afr. J. Ecol.* **43**, 91–96.

- Treves, A. (2000). Theory and method in studies of vigilance and aggregation. *Anim. Behav.* **60**, 711–722.
- Underwood, R. (1982). Vigilance behaviour in grazing African antelopes. *Behaviour* **79**, 81–107.
- Walther, F.R., Mungall, E.C. & Grau, G.A. (1983). Male behavior at peak of territoriality. In: *Gazelles and their relatives*: 90–171. New Jersey: Noyes Publications.
- Yaber, M.C. & Herrera, E.A. (1994). Vigilance, group size and social status in capybaras. *Anim. Behav.* **48**, 1301–1307.
- You, Z. & Jiang, Z. (2005). Courtship and mating behaviors in Przewalski's gazelle *Procapra przewalskii*. *Acta Zool. Sinica* **51**, 187–194.