

Interference competition and group size effect in sika deer (*Cervus nippon*) at salt licks

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Abstract Competition has long been considered as a confounding factor of group size effect but the understanding of interference competition is rudimentary for the difficulty in disentangling interference competition from scramble competition adequately. Here, we analysed remote-camera video records of wild sika deer (*Cervus nippon*) at salt licks in southern China from March 1, 2006 to November 30, 2008 to investigate how interference competition and predation risk interacted on vigilance behaviour. Scramble competition is negligible at salt licks; therefore, we could focus our interest in interference competition. We used linear mixed model to compare vigilance, licking and aggression behaviours among females with and without fawn as well as males with different group sizes to identify the primary role of vigilance behaviour in sika deer. In total, 168 individuals were recorded and observation time was 2,733.04 min. We found that deer spent much time on vigilance and scanned frequently in spring and winter, and females with fawn spent more time on vigilance than females without fawn, suggesting vigilance for predation risk. Aggression ratio

increased first and then decreased, while scan frequency continued to decline and then slightly increased when group size increased from two to seven, implying vigilance for interference competition. Our results suggested vigilance in sika deer was influenced by both predation risk and interference competition, but was mainly driven by predation risk even at sites with intense interference competition. Our results of interference competition shed some light on finding the underlying mechanism of group size effect in wild populations.

Keywords Bait site · Group size effect · Interference competition · Licking behaviour · Predation risk · Vigilance behaviour

Introduction

Vigilance has largely been attributed to detect predation threats. However, other benefits such as keeping track of mates, avoiding conspecific aggression, or exploring new food items may also be reasons for vigilance (Burger and Gochfeld 1994; Treves 2000; Fortin et al. 2004). The prediction that vigilance should decrease with group size (known as group size effect) has been tested extensively both in laboratory and in the field (Roberts 1996; Beauchamp 2008). Over the past few decades, group size effect is mainly explained by anti-predator consideration through ‘many-eyes’ hypothesis or dilution hypothesis (Elgar 1989; Delm 1990; Lima 1995; Roberts 1996; Beauchamp 2008). However, several confounding factors are found to modulate the effect of group size on vigilance in recent researches (Cresswell 1997; Barbosa 2002; Beauchamp and Ruxton 2003; Bednekoff and Lima 2005; Beauchamp 2009).

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A commonly mentioned confounding factor is competition. Competition may be a result of scramble (also known as exploitative), where one individual removes resources and leaves less for others, or interference (also called contest), where the presence of one individual impedes the access of resources by others. These two kinds of competition are both considered as confounding factors of group size effect in previous reviews (Elgar 1989; Beauchamp 2003). The potential influence of scramble competition on vigilance has long been recognized (Beauchamp and Livoreil 1997; Lima et al. 1999; Beauchamp and Ruxton 2003). However, the understanding of interference competition remains limited since behaviours underlying it are complex and it is difficult to disentangle interference competition from scramble competition adequately (Smallegange et al. 2006; Vahl et al. 2005; Nakayama and Fuiman 2010). Interference competition induces high vigilance due to the need to monitor both predators and competitors for possible threatening (Cresswell 1997; Beauchamp 2003; Sansom et al. 2008). In most organisms, the intensity of interference competition is measured through time spent in agonistic interaction (Smallegange et al. 2006; Nakayama and Fuiman 2010).

Bait sites are commonly considered as dangerous places since both hiding places and the behaviour of potential prey are likely known to predators (Burger and Gochfeld 1992; Moe 1993). In addition, sodium is clumped at artificial salt licks and is a defensible resource. The centres of salt licks are usually rich in sodium. Individuals at salt licks face great competition and even fight for the centre place of salt licks. Sodium salts are plenty over short time period; therefore, scramble competition is negligible at salt licks. Seasonal pattern of lick use has been found on sika deer (*Cervus nippon*), and there is sexual difference in lick use (Ping et al. 2010). Thus, salt licks were ideal sites to identify how interference competition and predation risk interacted on vigilance behaviour in sika deer.

Here, we used remote-camera videos to record behaviours of wild sika deer. We examined vigilance, licking and aggression behaviour over different group size, group composition and season. We aimed to identify the primary role vigilance behaviour played at sites with intense competition. We tested two hypotheses that sika deer vigilance served to detect predation risk or conspecific competition. If vigilance serves to detect predation risk, we then expect that vigilance time should decrease and licking time should increase with increasing group size and females with fawn should spend more time vigilance than other groups since juveniles are killed more often than other group members (Burger and Gochfeld 1994; Laundré et al. 2001; Childress and Lung 2003; Wolff and Van Horn 2003); on the other hand, if vigilance behaviour serves to monitor conspecific competition, we then expect that vigilance time and

aggression time should increase with group size, and no significant difference should be seen between females with fawn and other groups.

Materials and methods

Study site

Our study was carried out at Taohongling Sika Deer National Nature Reserve (29°42'–29°53'N, 116°32'–116°43'E) in Pengze County, Jiangxi Province, China. The reserve is 125 km² in area with an altitude ranging from 30 to 536 m above sea level. Climate of this area belongs to subtropical humid type. Average annual temperature is 15.1°C and annual precipitation is 1,300 mm (Jiang 2009). Four seasons are defined as spring, March–May; summer, June–August; autumn, September–November and winter, December–February (Natural Geography Chronicles Compiling Committee of Jiangxi Province 2003). Vegetations are composed of tall grasses, forbs and secondary growth of shrub species. Besides these, there are small patches of deciduous broad-leaved and evergreen-deciduous mixed forests inside the reserve (Liu 2007). Wild animals in the reserve include 44 species of mammals, 173 species of birds, 19 species of amphibian, 29 species of reptile and 29 species of fishes (Jiang 2009). Predators of sika deer in our study area include wolf (*Canis lupus*), Asian wild dog (*Cuon alpinus*) and leopard (*Panthera pardus*, Wang 1999).

Artificial salt licks

In August 2003, seven sites where sika deer was frequently sighted were chosen to place artificial salt licks. The licks were 4 to 9 m² in area, with distance of about 1 km from each other. After clearing the above ground vegetation, 10 kg of sodium salts were mixed evenly with the surface soil. Salts were supplemented every 6 months. Sika deer began to visit salt licks in September 2003, and from then on, they used the salt licks frequently. Many other species in this reserve used artificial salt licks, including reeve's muntjac (*Muntiacus reevesi*), wild boar (*Sus scrofa*) and some birds. Besides that, leopard was also recorded wandering around salt licks.

Video recording

Remote monitor video cameras were placed in waterproof boxes and mounted on poles about 16 m high and 60–80 m away from salt licks at the same time as the artificial salt licks were established. The cameras were controlled by a computer and could scan around. Solar-powered batteries (12 V) which were placed on one side of poles were used to supply power to cameras. Optical signal was sent to

receivers by fibre optic cables and was recorded as videos in hard disks of a computer in the ecological station of the nature reserve. The recorder was programmed in real-time mode and could record date, time and licking place on the disks. The export files were *.MPG format. The cameras were routinely checked every fortnight.

We collected data once every 5 days during daylight (0500–1900 hours in spring and summer, 0600–1800 hours in autumn and winter) from March 1, 2006 to November 30, 2008. The video recording began when the first deer individual in a group walked into salt licks and terminated when the last individual in a group stepped out of salt licks.

Video replaying

The videos were replayed on a computer in the laboratory, and the software named Timer (programmed by a colleague in Institute of Zoology, Chinese Academy of Sciences) was used to record frequency and duration of each behaviour of focal individual. We used all-occurrence sampling method to record beginning and ending time of all behaviours and took note of group size and group composition. All the videos were reviewed by the same person. We classified seven behaviours as follows:

- Licking: standing or walking slowly with head down at salt licks, taking bites
- Vigilance: staring, alerting or scanning its surroundings with head up and ears cocked
- Aggression: chasing, biting, bumping other group members with head raised or rearing and kicking other group members with two forelegs
- Resting: lying on the ground, ruminating or nodding
- Moving: walking or running
- Grooming: licking or scratching itself or other group members
- Others: uncommon behaviours displayed by few sika deer

We focused on one focal individual during each replaying of the video records. When two or more individuals used the same salt lick together, we replayed the videos to record behaviours of every individual and noted down the originator and receiver of social behaviour. The deer in this study were not individually recognizable, thus, we might have observed the same individual more than once. However, these cases of multiple observations would not likely to bias our conclusion from the statistical analyses for the probability of sampling the same individual was only $0.47 \pm 0.048\%$ (95% confidence limit).

Data analyses

We divided deer groups into females with fawn, females without fawn, males and mixed-sex groups according to

previous study (Monteith et al. 2007). Mixed-sex groups were rarely recorded, thus, we focused on females with fawn, females without fawn and males to analyse. Only adult individual number was counted as group size when there were fawns in the group. Since increase in vigilance or licking can be achieved by either frequency or duration, we measured all these variables in our analyses. Scan/lick frequency was defined as the average number of scans/licks per individual per minute, and scan/lick duration as average duration of every scan/lick in a video record. Vigilance/licking time was calculated by time spent on vigilance/licking divided by time spent on all behaviours by one individual in a video. Aggression ratio was calculated by time spent on aggression divided by time spent on all behaviours by one individual in a video. Staying time was the entire period of occupancy of the salt licks area for focal individual in one visit. Observation time was the time period of active behaviour for focal individual in one visit. When the situation that deer individuals were taking rest at salt licks came, frequency, duration and ratio were calculated as number/active minutes.

We compared scan frequency, scan duration, vigilance time, lick frequency, lick duration, licking time and aggression ratio among groups of different sizes and compositions at salt licks. All statistical analyses were performed with SPSS 15.0 for Windows (SPSS Inc., Chicago). We used the Kolmogorov–Smirnov test to check the normality of data. Scan frequency and lick frequency were square-root transformed, scan duration, lick duration, vigilance time, licking time and aggression ratio were \ln transformed to meet assumptions of normality and homogeneity of variances. Licks differ in predation risk and distance from concealment which are known to affect vigilance and group size effect (Beauchamp 2010). Thus, we used linear mixed model to assess the effect of group size, group composition and season on scan frequency, scan duration, lick frequency, lick duration, vigilance time, licking time and aggression ratio with group size, group composition and season as fixed factors and lick place as a random factor. Group size, group composition, season and the interaction between group size and group composition, group size and season were included in the model. Fisher's least significant difference pair-wise comparison was used to compare the differences between individuals in groups of different sizes, compositions and interaction between group size and group composition. All values were presented as untransformed means \pm SE. All statistical tests were two-tailed, and $P < 0.05$ was considered statistically significant.

Results

Thirty-three females with fawn (512.57 min), 96 females without fawn (1,600.23 min) and 39 males (620.24 min)

were recorded at salt licks. The total observation time was 2,733.04 min. The mean staying time of sika deer at salt licks was 21.01 ± 1.44 min with range between 1.16 and 135.46 min, and the mean observation time was 16.27 ± 0.96 min with range between 0.81 and 71.94 min. Mean group size was 1.49 ± 0.07 with numbers varying from one to seven.

Deer spent more time licking and less time on vigilance when group size increased (Figs. 1 and 2), but the differences were not significant ($F_{4, 153} = 1.369$, $P = 0.247$ for vigilance time and $F_{4, 153} = 0.843$, $P = 0.500$ for licking time). Aggression ratio increased first and then decreased while scan frequency continued to decline and increased slightly when group size increased from two to seven (Fig. 3). No significant group size effect could be found on aggression ratio ($F_{3, 20} = 0.439$, $P = 0.728$) and scan frequency ($F_{4, 153} = 1.344$, $P = 0.256$). Deer in smaller groups scanned more frequently (1.19 ± 0.065 number of scans per minute for individuals in group size of one) than individuals in larger groups (0.779 ± 0.117 number of scans per minute for individuals in group size of four, $P = 0.011$), and spent more time on vigilance ($29.40 \pm 1.68\%$ for individuals in group size of one) than individuals in larger groups ($13.55 \pm 5.74\%$ and $8.32 \pm 1.48\%$ for individuals in group size of four and seven; $P = 0.023$, $P = 0.036$). No significant difference could be found on scan duration ($F_{4, 153} = 0.546$, $P = 0.702$), lick frequency ($F_{4, 153} = 0.445$, $P = 0.776$) and lick duration ($F_{4, 153} = 0.517$, $P = 0.724$) of deer individuals with different group sizes.

There was no significant effect of group composition on vigilance time ($F_{2, 153} = 1.054$, $P = 0.351$) and licking time ($F_{2, 153} = 0.933$, $P = 0.396$). Pair-wise comparisons showed

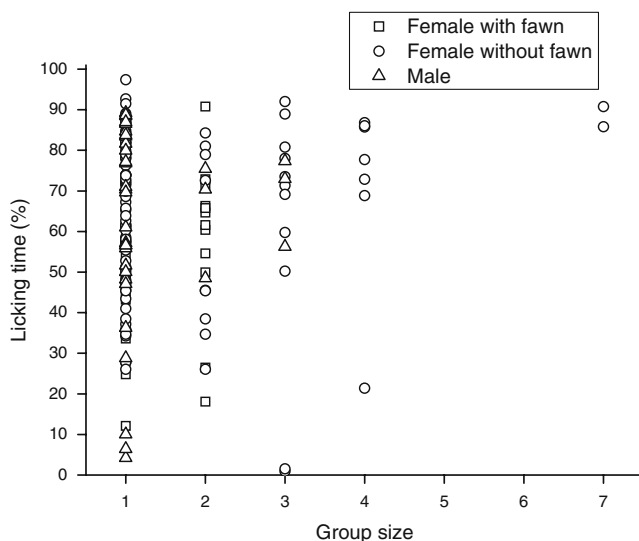


Fig. 1 Licking time of sika deer individuals with different group sizes and group compositions. There was no significant group size effect on licking time (linear mixed model, $F_{4, 153} = 0.843$, $P = 0.500$)

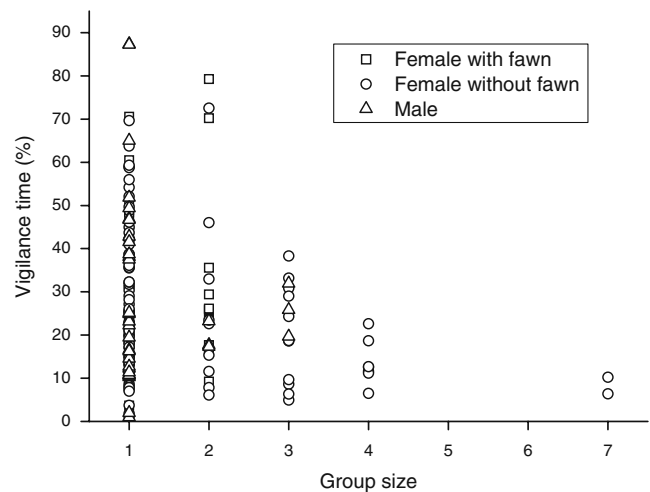


Fig. 2 Vigilance time of sika deer individuals with different group sizes and group compositions. There was no significant group size effect on vigilance time (linear mixed model, $F_{4, 153} = 1.369$, $P = 0.247$)

that females without fawn spent less time on vigilance ($21.05 \pm 2.35\%$) and more time licking ($69.62 \pm 3.04\%$) than females with fawn ($27.77 \pm 4.14\%$ and $62.59 \pm 5.36\%$, $P = 0.005$ and $P = 0.014$). No significant difference could be found among groups with different composition on aggression ratio ($F_{2, 20} = 0.837$, $P = 0.449$), scan frequency ($F_{2, 153} = 0.741$, $P = 0.478$), scan duration ($F_{2, 153} = 0.573$, $P = 0.565$), lick frequency ($F_{2, 153} = 1.057$, $P = 0.350$) and lick duration ($F_{2, 153} = 0.123$, $P = 0.884$).

There were significant effects of season on time spent on vigilance ($F_{3, 153} = 4.408$, $P = 0.005$), scan frequency ($F_{3, 153} = 10.407$, $P < 0.001$), lick frequency ($F_{3, 153} = 9.314$, $P < 0.001$) and lick duration ($F_{3, 153} = 7.167$, $P < 0.001$). Deer individuals

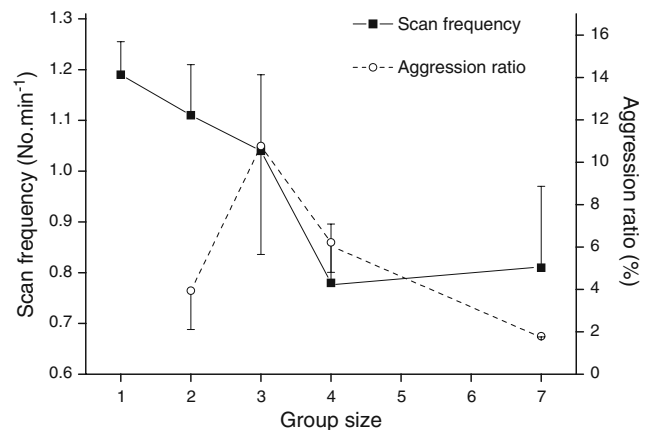


Fig. 3 Scan frequency and aggression ratio of sika deer individuals with different group sizes. Aggression ratio declined first and then increased slightly while scan frequency decreased first and then increased when group size increased from two to seven and no significant effect could be found (linear mixed model, $F_{4, 153} = 1.344$, $P = 0.256$ for scan frequency and $F_{3, 20} = 0.439$, $P = 0.728$ for aggression ratio). Plus error bar was presented for scan frequency, and minus error bar was given for aggression ratio

scanned frequently and spent much time on vigilance in spring (1.30 ± 0.095 number of scans per minute, $27.40 \pm 2.53\%$) and winter (1.29 ± 0.26 number of scans per minute, $24.38 \pm 6.98\%$). Lick frequency of individual was highest in winter (1.57 ± 0.29 number of licks per minute) and lowest in autumn (0.89 ± 0.18 number of licks per minute). Lick duration of individual was high in summer (56.23 ± 14.24 s) and autumn (47.24 ± 9.74 s) and low in winter (28.24 ± 15.51 s). The interaction between group size and group composition, group size and season and the random factor of lick place had no significant effect on all variables we investigated.

Discussion

Our results suggested that vigilance in sika deer was affected by both predation risk and interference competition, but mainly functioned to detect predation risk even at sites with intense competition. Vigilance behaviour has been found to be influenced by both predation risk and conspecific competition in many taxa (Lima et al. 1999; Treves 2000; Blumstein et al. 2001; Hirsch 2002; Lung and Childress 2007; Favreau et al. 2010), and interference competition may be high enough to counter the vigilance benefit in large groups (Cresswell 1997; Blumstein et al. 2001).

Individuals spent much time on vigilance and scanned frequently in spring calving season and winter, the two periods with high predation risk. Females with fawn spent more time on vigilance than females without fawn. These two findings confirmed the predation risk hypothesis. Deer individuals are in poor body condition and are vulnerable in winter. Male elk lose as much as 20% of their pre-rut body mass by mid-November and continue to lose weight throughout the winter, and females also lose 10% of body mass throughout winter (Winnie, Jr. and Creel 2007). The presence of offspring has a dramatic effect on the vigilance behaviour of the mothers in both mammals and birds (Elgar 1989). Females with young often spend more time on vigilance than other groups, since juveniles are vulnerable to predators and mothers have to respond to potential predation risk most quickly and significantly (Laundré et al. 2001; Lung and Childress 2007; Li et al. 2009).

Sodium is clumped at the centre of salt licks with small area and individuals compete for best licking place. Aggression ratio increased when group size increased from two to four and decreased when group size was seven while scan frequency decreased first and then increased when group size increased from two to seven. These findings suggested there was interference competition at salt licks and deer scanned to monitor conspecifics in some circumstances. The costs of agonistic interactions include not just loss of fitness through injury or death but also energy and

time expenditure (McPeck and Crowley 1987; Nakayama and Fuiman 2010). Thus, individuals will increase monitoring of conspecifics to avoid fighting. Avoidance of direct aggression of interference interactions has been illustrated in many studies (Case and Gilpin 1974; Carothers and Jaksić 1984). The increased scan frequency in sika deer might be used to avoid possible agonistic interactions when group size was seven. Individuals in large groups tend to space themselves farther apart, resulting in a decline in aggression, which has been found in mule deer (*Odocoileus hemionus*; Bowyer et al. 2001). The decline in aggression in large groups of sika deer might also be caused by spacing effect.

Deer individuals decreased time spent on vigilance and increased licking time with increasing group size; however, no significant group size effect could be found. This might be explained by the balance between extra-group vigilance (predation risk) and intra-group vigilance (interference competition) which changed in opposite direction with group size. The higher competition for the best licking place countered some vigilance benefits in larger groups. Vigilance was mainly driven by predation risk given the trend of decreased vigilance when group size increased. These results were consistent with the study on dark-eyed juncos (*Junco hyemalis*) that competition might influence vigilance in some circumstances, but the driving force of group size effect was predation risk (Lima et al. 1999).

It is possible that bold individuals would use the salt licks more often since personality affects the behaviour syndrome of animals, and bold individuals are more explorative than shy ones (Wolf et al. 2007; Garamszegi et al. 2009). This was exactly what we were concerned about before the study. Therefore, we did not take video records immediately after salt licks were established but after more than 2 years when deer became accustomed to salt licks to minimize the sampling error of more bold individuals in our videos. No significant effect of interaction between group size and group composition could be found on vigilance and licking time. Vigilance and licking time varied greatly in solitary individuals which might be caused by pooling data of females with fawn and other groups together. The high vigilance level of females with fawn might induce the variation.

The remote video cameras are helpful in wildlife behaviour study. Wherever, there might be some cases when some individuals in large groups are out of field, which might cause some error in the analysis. Remote video cameras are mounted on high poles far away from salt licks and can scan around by manually control, thus, the view fields of the video cameras are large. Besides that, the group size of sika deer in the reserve are small with mean group size of 2.2, ranging from one to eight (Fu 2006). Therefore, in most cases, we can record the whole group of

sika deer. Agonistic behaviour is often used to measure intensity of interference competition; however, other reasons, including establishing dominance and holding territory, are probable causation of aggression as well (Brown 1969; Drews 1993). Nevertheless, it was difficult to distinguish aggression used for interference competition and social dominance in the wild.

In conclusion, salt licks are peculiar for defensible and clumped sodium, negligible scramble competition and high predation risk, which serve as ideal sites to understand the interaction between interference competition and predation risk on vigilance behaviour. Our results suggested that vigilance in sika deer was influenced by both predation risk and interference competition, but was mainly driven by predation risk even at sites with intense competition. Our results of interference competition among individuals at salt licks shed some light on underlying mechanism of group size effect in wild sika populations. Interference competition and predation risk interact on vigilance behaviour but to what extent interference competition would affect vigilance behaviour is still an open question and needs further studies.

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References

- Barbosa A (2002) Does vigilance always covary negatively with group size? effects of foraging strategy. *Acta Ethol* 5:51–55
- Beauchamp G (2003) Group-size effects on vigilance: a search for mechanisms. *Behav Process* 63:111–121
- Beauchamp G (2008) What is the magnitude of the group-size effect on vigilance? *Behav Ecol* 19:1361–1368
- Beauchamp G (2009) How does food density influence vigilance in birds and mammals? *Anim Behav* 78:223–231
- Beauchamp G (2010) Relationship between distance to cover, vigilance and group size in staging flocks of semipalmated sandpipers. *Ethology* 116:645–652
- Beauchamp G, Livoreil B (1997) The effect of group size on vigilance and feeding rate in spice finches (*Lonchura punctulata*). *Can J Zool* 75:1526–1531
- Beauchamp G, Ruxton GD (2003) Changes in vigilance with group size under scramble competition. *Am Nat* 161:672–675
- Bednekoff PA, Lima SL (2005) Testing for peripheral vigilance: do birds value what they see when not overtly vigilant? *Anim Behav* 69:1165–1171
- Blumstein DT, Daniel JC, Evans CS (2001) Yellow-footed rock-wallaby group size effects reflect a trade-off. *Ethology* 107:655–664
- Bowyer RD, McCullough DR, Belovsky GE (2001) Causes and consequences of sociality in mule deer. *Alces* 37:371–402
- Brown JL (1969) Territorial behavior and population regulation in birds: a review and re-evaluation. *Wilson Bull* 81:293–329
- Burger J, Gochfeld M (1992) Effect of group size on vigilance while drinking in the coati, *Nasua narica* in Costa Rica. *Anim Behav* 44:1053–1057
- Burger J, Gochfeld M (1994) Vigilance in african mammals: differences among mothers, other females, and males. *Behaviour* 131:153–169
- Carothers JH, Jaksic FM (1984) Time as a niche difference: the role of interference competition. *Oikos* 42:403–406
- Case TJ, Gilpin ME (1974) Interference competition and niche theory. *P Natl Acad Sci USA* 71:3073–3077
- Childress MJ, Lung MA (2003) Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? *Anim Behav* 66:389–398
- Cresswell W (1997) Interference competition at low competitor densities in blackbirds *Turdus merula*. *J Anim Ecol* 66:461–471
- Delm MM (1990) Vigilance for predators: detection and dilution effects. *Behav Ecol Sociobiol* 26:337–342
- Drews C (1993) The concept and definition of dominance in animal behaviour. *Behaviour* 125:283–313
- Elgar MA (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol Rev* 64:13–33
- Favreau F, Goldizen AW, Pays O (2010) Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. *P Roy Soc B-Biol Sci* 277:2089–2095
- Fortin D, Boyce M, Merrill E, Fryxell J (2004) Foraging costs of vigilance in large mammalian herbivores. *Oikos* 107:172–180
- Fu YQ (2006) Study on population number, social structure, habitat utilization and auditory communication in sika deer (*Cervus nippon kopschi*) in Taohongling Nature Reserve. Dissertation, Xihua Normal University (In Chinese with English Abstract), China
- Garamszegi LZ, Eens M, Török J (2009) Behavioural syndromes and trappability in free-living collared flycatchers, *Ficedula albicollis*. *Anim Behav* 77:803–812
- Hirsch B (2002) Social monitoring and vigilance behavior in brown capuchin monkeys (*Cebus apella*). *Behav Ecol Sociobiol* 52:458–464
- Jiang Z (2009) Biodiversity and sika deer in the Taohongling Nature Reserve, Jiangxi, China. Tsinghua University Press, Beijing, In Chinese with English summary
- Laundré J, Hernández L, Altendorf K (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, Beauchamp G (2009) Vigilance in Przewalski’s gazelle: effects of sex, predation risk and group size. *J Zool* 277:302–308
- Lima SL (1995) Back to the basics of anti-predatory vigilance: the group-size effect. *Anim Behav* 49:11–20
- Lima SL, Zollner PA, Bednekoff PA (1999) Predation, scramble competition, and the vigilance group size effect in dark-eyed juncos (*Junco hyemalis*). *Behav Ecol Sociobiol* 46:110–116
- Liu J (2007) Food and habitat selection by sika deer (*Cervus nippon kopschi*) and habitat improvement in the Taohongling Nature Reserve, Jiangxi. Dissertation, Institute of Zoology, Chinese Academy of Sciences, China. (In Chinese with English Abstract)
- Lung MA, Childress MJ (2007) The influence of conspecifics and predation risk on the vigilance of elk (*Cervus elaphus*) in Yellowstone National Park. *Behav Ecol* 18:12–20
- McPeck MA, Crowley PH (1987) The effects of density and relative size on the aggressive behaviour, movement and feeding of damselfly larvae (Odonata: Coenagrionidae). *Anim Behav* 35:1051–1061

- Moe SR (1993) Mineral-content and wildlife use of soil licks in southwestern Nepal. *Can J Zool* 71:933–936
- Monteith KL, Sexton CL, Jenks JA, Bowyer RT (2007) Evaluation of techniques for categorizing group membership of white-tailed deer. *J Wildl Manage* 71:1712–1716
- Nakayama S, Fuiman LA (2010) Body size and vigilance mediate asymmetric interference competition for food in fish larvae. *Behav Ecol* 21:708–713
- Natural geography chronicles compiling committee of Jiangxi Province (2003) *Natural Geography Chronicles of Jiangxi Province*. Fangzhi, Beijing, China, In Chinese
- Ping X, Li C, Jiang Z, Liu W, Zhu H (2010) Sexual difference in seasonal patterns of salt lick use by south China sika deer *Cervus nippon*. *Mamm Biol*. doi:10.1016/j.mambio.2010.11.001
- Roberts G (1996) Why individual vigilance declines as group size increases. *Anim Behav* 51:1077–1086
- Sansom A, Cresswell W, Minderman J, Lind J (2008) Vigilance benefits and competition costs in groups: do individual redshanks gain an overall foraging benefit? *Anim Behav* 75:1869–1875
- Smallegange IM, Van Der Meer J, Kurvers R (2006) Disentangling interference competition from exploitative competition in a crab–bivalve system using a novel experimental approach. *Oikos* 113:157–167
- Treves A (2000) Theory and method in studies of vigilance and aggregation. *Anim Behav* 60:711–722
- Vahl WK, Lok T, Van Der Meer J, Piersma T, Weissing FJ (2005) Spatial clumping of food and social dominance affect interference competition among ruddy turnstones. *Behav Ecol* 16:834–844
- Wang H (1999) *Wildlife conservation in rural southeastern China: wildlife harvest and the ecology of sympatric carnivores*. Dissertation, University of Massachusetts
- Winnie J Jr, Creel S (2007) Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. *Anim Behav* 73:215–225
- Wolf M, Van Doorn GS, Leimar O, Weissing FJ (2007) Life-history trade-offs favour the evolution of animal personalities. *Nature* 447:581–584
- Wolff J, Van Horn T (2003) Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. *Can J Zool* 81:266–271