

Seasonal and sexual variation in vigilance behavior of goitered gazelle (*Gazella subgutturosa*) in western China

Canjun Xia · Wenxuan Xu · Weikang Yang ·
David Blank · Jianfang Qiao · Wei Liu

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Abstract Animals receive benefits from social behavior. As part of a group, individuals spend less time having to be vigilant. This phenomenon, called the “group size effect,” is considered the most dominant factor in an animal’s demonstrated level of vigilance. However, in addition to group size, many other social and environmental factors also influence the degree of vigilance, including the season of the year and the sex of the individual. In our study, we examined the vigilant behavior of goitered gazelles in the Xinjiang Province in western China to test whether and how seasons, the yearly breeding cycle, and group size affect vigilance. According to our results, we found that seasonal factors were not a substantial influence on a gazelle’s level of vigilance, while group size had a tangible effect. In comparison, the yearly breeding cycle (a natural phenomenon) was the most powerful factor: it significantly changed the degree of vigilance in females during birthing and males during rut. Anthropogenic factors (unnatural phenomena) were also potential causes of increased vigilance in both sexes during winter.

Keywords Anti-predator behavior · Group size · Vigilance · Rutting behavior · Birth season

Introduction

Vigilance requires time and visual attention, and both are limited resources (Dukas 1998). Consequently, an animal’s vigilance conflicts with other activities, such as grooming and fighting, and especially feeding (Caraco 1979; Isbell and Young 1993; Mooring and Hart 1995; Brick 1998). Although some experiments suggest that vigilance is not completely impaired in feeding animals (Lima and Bednekoff 1999), the conflict between feeding and vigilance is a classic behavioral trade-off (Pulliam et al. 1982). Since feeding behavior over seasons varies with the change in an individual gazelle’s biomass, time spent feeding decreases when food is abundant, or—conversely—increases when food is poor. The trade-off between feeding and vigilance, then, should change the duration of these activities (Pulliam et al. 1982); time spent being vigilant has to adjust to changes in biomass.

Studies on vigilance have shown sex to be an important factor influencing vigilant behavior (Hunter and Skinner 1998; Cameron and Du Toit 2005; Michelena et al. 2006; Li and Jiang 2008). Although several studies have shown that the vigilance levels are usually different between females and males, reports have not suggested any consistent pattern regarding the more vigilant sex (Elgar 1989; Laundre et al. 2001; Cameron and Du Toit 2005). For example, in impala, breeding males are more vigilant, as they spend extra time defending their “harem” and looking out for rival males (Shorrocks and Cokayne 2005), whereas in Tibetan gazelle (*Procapra picticaudata*), females are more vigilant than males because females are more

C. Xia · W. Xu · W. Yang (✉) · D. Blank · J. Qiao
Key Laboratory of Biogeography and Bioresource in Arid Land,
Xinjiang Institute of Ecology and Geography,
Chinese Academy of Sciences, Urumqi 830011, China
e-mail: Yangwk@ms.xjb.ac.cn

C. Xia · W. Xu
Graduate University, Chinese Academy of Sciences,
Beijing 100049, China

W. Liu
School of Life Sciences, Sichuan University,
Chengdu 610064, China

vulnerable to predators, especially when they have lambs to nurse (Li and Jiang 2008). Childress and Lung (2003) found that females with young are the most vigilant members of a herd, because predators prefer to prey on their young.

Most ungulate species are gregarious by nature. The advantages and possible disadvantages of living in big groups is a popular subject in behavioral ecology (Elgar 1989; Quenette 1990; Roberts 1996; Frid 1997; Brashares and Arcese 2002; Dias 2006; Li and Jiang 2008; Li et al. 2009). The phenomenon of a negative correlation between vigilance intensity and group size was termed the “group size effect.” This negative relationship can be interpreted in three different ways. First, more eyes are available in large groups to scan the surrounding landscape, thus allowing individuals to be alerted to predators earlier and more easily; individuals are able to decrease their own vigilance and benefit from the alertness of other group members, which is called the detection effect or the “many eyes” hypothesis (Pulliam 1973). Second, predators usually select only one prey animal during an attack, so individuals in large groups are less likely to be killed than individuals in smaller groups; the risk is diluted. As a result, individuals in large groups can allocate more of their time to other activities. This is called the dilution effect or the “safety in numbers” hypothesis (Cresswell 1994). Third, there is the “scramble competition” hypothesis, which focuses on competition for limited resources being more aggressive within larger groups, which, in turn, leads to a decrease in vigilance (Beauchamp and Ruxton 2003).

It has been found, however, that the group size effect is not typical for all mammals (Treves 2000; Laundre et al. 2001; Barbosa 2002; Cameron and Du Toit 2005; Shorrocks and Cokayne 2005). For example, female impala (*Aepyceros melampus*) spend less time being vigilant and more time feeding as their group size increases, but territorial males showed no significant changes in vigilance with increasing group size because of the time spent watching their females and looking out for rival males (Shorrocks and Cokayne 2005). Li et al. (2009) suggested that vigilance aimed at rivals or mates may increase with group size in males. Therefore, the functional interpretation of the group size effect remains poorly understood. Studies on the effects of group size should be conducted in more species to explore whether and why these effects take place.

Vigilant behaviors have been documented for some gazelle species (Fitzgibbon 1990a, b; Manor 2001; Li and Jiang 2008; Li et al. 2009). For example, immature Thomson’s gazelles (*Gazella thomsoni*) usually either hide or assume a prone response as anti-predator strategies due to their inability to outrun predators (Fitzgibbon 1990c). Manor and Saltz (2003) studied how varying levels of

human disturbance influenced the time that mountain gazelle (*Gazella gazella*) devoted to vigilance in different group sizes. Some descriptive information on the vigilance behavior of goitered gazelles from Turkmenistan and Kazakhstan (Gorelov 1972; Zhevnerov 1984) is available, but in the present work we provide a quantitative analysis of this phenomenon for the first time.

Here, we used the goitered gazelle, *Gazella subgutturosa* (Güldenstaedt 1780), as a study animal to test the group size effect and examine its possible changes over seasons and between males and females. According to theory and results from other studies, we hypothesized that gazelles would spend more time being vigilant in summer due to an abundance of food, and less time being vigilant in winter because of a lower quality and a lower density of suitable food. The vigilance level for females in summer was predicted to be higher than that for males, because females with young are the more alert members in a group. The vigilance level for males in winter was predicted to be higher than that for females, since males spend more time on social behaviors that can increase their vigilance level. We also hypothesized that goitred gazelles would be more vigilant in smaller groups than in larger groups for both sexes, and across all seasons, according to the “group size effect.”

Materials and methods

Study area

This study was conducted in the Kalamaili Mountain Ungulate Nature Reserve (44°36′–46°00′N, 88°30′–90°03′E), located in the eastern part of Junggar Basin, Xinjiang, China. This area and the adjacent regions of Mongolia are an important part of the range of goitered gazelles. It once supported the largest population of the subspecies *G. s. hillieriana*; now about 7,000–20,000 goitred gazelles live in this reserve (Chu et al. 2009). The reserve covers 1.8×10^4 km² of arid plains and hills with an average elevation of ca. 1,000 m above sea level, and a range from 600 to 1,470 m. The local climate is a harsh continental-type environment with an average yearly temperature of +1.99°C, which is lower than that for Central Asia, but higher than that in northern Mongolia. Winter is long and cold with uneven snow cover (thin on the hills and deep on the plains); summer is hot and quite short. The average temperature in January is –24.3°C, with an absolute minimum of –45°C and maximum of +1.4°C. The average temperature in July is +20.5°C, with an absolute maximum of +38.4°C and a minimum of +6.0°C. Rainfall is most intense during spring and early summer, and precipitation varies from 100 to 300 mm a year in

different parts of the Junggar Basin (Unatov 1960). The Kalamaili Reserve has an average annual rainfall of 186.8 mm and an annual evaporation rate of 2,090.4 mm.

The climate system influences the vegetation of the region, which has a number of specific characteristics. In spring, ephemerals appear during the rainy period at the end of spring to early summer. Plant growth begins late, and the duration is short (only 180 days). Plants do not fade in summer, and they have only one dormant period in winter. Vegetation cover is quite sparse and consists mostly of desert shrubs (40–50 cm) and dwarf shrubs (10–15 cm) from the families *Chenopodiaceae*, *Ephedraceae*, *Tamaricaceae*, and *Zygophyllaceae* (Unatov 1960). The most common desert tree in the reserve is *Haloxylon ammodendron*. Common shrubs are *Anabasis salsa*, *Atraphaxis frutescens*, *Calligonum mongolicum*, *Ceratocarpus arenarius*, *Ceratoides lateens*, and *Reaumuria soongorica*. It is possible to find herbaceous species, mostly under patches of shrubs, and they include *Allium polyrhizum*, *Chorispora tenella*, *Stipa glareosa*, and some *Astragalus* species. Species from the genera *Sterigmotemum*, *Alyssum*, *Scorzonera*, *Erysimum*, *Eremurus*, *Sonchus*, and *Lappula* are common here.

Goitered gazelles and kulans (*Equus hemionus*) are the most common wild ungulate species in the Reserve; Argali (*Ovis ammon*) and reintroduced Przewalski's horses (*Equus przewalskii*) are the other large ungulates that can be seen here. In addition, about 2,000 herdsman and 200,000 livestock stay in the reserve during winter (Liu et al. 2008; Chu et al. 2008). The main predators of the goitered gazelle in the reserve are wolves and foxes, but the number of wolves is very low; foxes pose a predation threat exclusively to young within the first few days after birth (Blank 1992). During our study, we did not register any predators around the gazelles we observed, so the predation risk from wolves and foxes was not considered to have a direct influence on the vigilance behavior of the goitered gazelle. In China, the goitered gazelle is on the grade II list of state-protected animals, and any hunting of this animal is forbidden. Moreover, the law strictly prohibits individuals from keeping guns in China. Therefore, poaching is very rare inside the nature reserve.

Study species

Goitered gazelles are mid-sized antelopes that live in the semi-deserts and deserts of the Asian continent. The populations of this species have declined steadily in number throughout their range, due to poaching and other human activities that have resulted in habitat loss (IUCN 2010). The goitered gazelle is classified as vulnerable in the IUCN Red List. Four subspecies have been identified around the world (Groves 1969): *G. s. marica* (Thomas

1897), *G. s. hillieriana* (Heude 1894), *G. s. yarkandensis* (Blanford 1875), and *G. s. subgutturosa* (Groves 1985; Kingswood and Blank 1996; Mallon and Kingswood 2001; Mallon 2008). Two subspecies occur in China, *G. s. hillieriana* and *G. s. yarkandensis*, and live in very restricted areas in China and Mongolia. *G. s. yarkandensis* is distributed in the Tarim Basin, the Turpan Basin and Hami; *G. s. hillieriana*, which was observed during this study, is distributed in the Junggar Basin, Gansu, and Inner Mongolia (Yang et al. 2005).

Among these four subspecies, adult males generally have long horns of 203–340 mm. Females of some subspecies have short horns (Groves 1969, 1985; Zhevnerov 1984; Heptner et al. 1988). It was possible to distinguish adult males from subadult males according to the lengths of their horns, but we did not consider the differences in behavior between adult and subadult males. Goitered gazelles have a gregarious nature and usually occur in small groups, although it is possible to find herds that are numbered in the hundreds to thousands (Kingswood and Blank 1996; Baskin and Danell 2003; Qiao et al. 2008). They are polygamous; males court females most vigorously during rutting season, which occurs from mid-October through mid-December (Blank 1985; Kingswood and Blank 1996). The goiter-like swelling of the throat is an enlarged cartilaginous cylinder (Roberts 1977), and during rutting season, the throat swelling of territorial males increases noticeably in size (Zhevnerov and Bekenov 1983). Goitered gazelles migrate, following green pastures, even when water is abundant (Kingswood and Blank 1996).

Behavioral sampling

From 2007 to 2009, the behavior of the goitered gazelles was investigated using the focal animal sampling method (Altmann 1974). Binoculars (magnification 8×) and a telescope (magnification 20 × 60) were used for distance viewing. We defined seasons according to the classifications used by Xu et al. (2008) as follows: spring (April–May), summer (June–August), autumn (September–October) and winter (November–March). Observation periods were restricted to daytime hours in all seasons: 0800–2100 hours (spring), 0600–2200 hours (summer), 0800–1900 hours (autumn), and 0900–1900 hours (winter). During our study, 355.3 h were spent in the field, and 2,132 focal samples were taken from 531 groups in total. Group sizes ranged from 1 to 27 individuals.

Individuals were defined as being in a united group when distances between them were less than 50 m (Clutton-Brock et al. 1982). Individuals farther than 50 m from others were not considered part of that group. Solitary individuals were classified as a group of one rather than

single gazelles. We took samples from as many groups as possible, with only a few individuals from the same group being observed. In this way, we tried to reduce the possibility of pseudo-replication. For each sighting, the date, group size, and weather were recorded.

We randomly selected focal animals and made direct observations. Each gazelle was observed for 10 min. Samples that lasted less than 10 min because of a subject leaving the group or a change in the group size were excluded from our analysis. We recorded all behaviors of focal animals using Aigo voice recorders to ensure the accuracy of the behavioral data. All data were transformed to digital files by replaying the audio recordings. The percentage vigilance was obtained by dividing the amount of time spent being vigilant during a single sample by 10 min. Vigilance frequency represented the number of single vigilant acts per 10 min sample. Vigilance duration was the length of time for a single vigilant act. We calculated average indices of the percentage vigilance, vigilance frequency and vigilance duration across all focal observations for each sex and season. We observed gazelles from hidden positions at a distance of over 500 m, and took care to ensure that our subjects were not disturbed. If the animals were disturbed, behavioral recording was delayed until the gazelles appeared to be relaxed, or we abandoned this group and initiated a new sample. Five behavioral categories were defined: feeding, resting, vigilance, moving and “other” (lactation, courtship, grooming, drinking). A gazelle was categorized as feeding when it was standing or walking slowly with its head below shoulder level, biting or chewing plants, or if it was walking with its muzzle close to the ground. Resting was recorded if the gazelle was lying down. Vigilance was defined when a gazelle was scanning its surroundings or being motionless with its head at or above shoulder level. Moving was noted when the gazelle walked or ran with its head at or above shoulder level.

Statistical analysis

The percentage vigilance was square root transformed; vigilance duration and frequency were first log-transformed, and then the data were tested for normality using a Kolmogorov–Smirnov test. All data were normally distributed, and a one-way ANOVA was used to test the effects of season on the percentage vigilance, vigilance duration and frequency. If a significant difference was found in the effects of seasons, then a post hoc multiple comparison procedure (Fisher’s LSD) was used to test for differences between seasons. The independent sample *t* test was used to test for possible differences between females and males in each season. We used Spearman’s rank correlation tests to analyze the correlation between group size

and vigilance (Childress and Lung 2003). All statistical analyses were carried out using the SPSS13.0 software package.

Results

Seasonal and sexual differences

For females, the percentage vigilance was highest in summer (6.9%) and winter (7.0%); for males, it was highest in winter (19.2%) and lowest in summer (2.8%) (Fig. 1a). The one-way ANOVA showed that the season had a considerable effect on the percentage vigilance in both females ($F = 12.5$, $df = 3$, $P < 0.001$) and males ($F = 118.8$, $df = 3$, $P < 0.001$). The post hoc comparisons showed that significant differences were found among seasons in females, except between summer and winter,

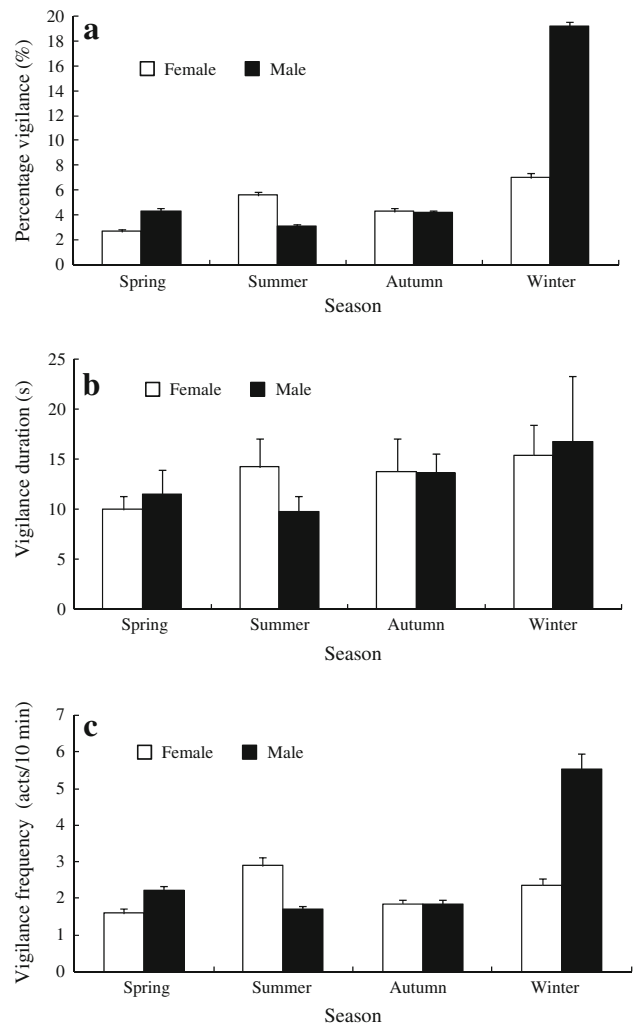


Fig. 1 Effect of season and sex on the percentage vigilance (a), duration (b) and frequency (c) (mean \pm SE)

and the difference was significantly higher in males in winter than in any other season (Fig. 1a). We did not find a significant difference between males and females in spring and autumn. However, females were more vigilant than males in summer (Table 1), and males were more vigilant than females in winter (Table 1).

The longest vigilance duration was recorded in winter for both females (15.4 s) and males (16.7 s) (Fig. 1b). The one-way ANOVA showed a significant difference in vigilance duration among all seasons for both females ($F = 16.0$, $df = 3$, $P < 0.05$) and males ($F = 33.8$, $df = 3$, $P < 0.05$). The post hoc comparisons showed that the duration of vigilance was significantly different among all seasons, except between summer and autumn in females and between spring and summer in males (Fig. 1b). Significant differences between males and females were found in summer and winter (Table 1), but no significant differences were found in spring and autumn (Table 1).

The average vigilance frequency was highest in summer for females (2.9 times per 10 min) and in winter for males (5.5 times per 10 min) (Fig. 1c). The one-way ANOVA showed that season affected the vigilance frequency for both females ($F = 6.4$, $df = 3$, $P < 0.001$) and males ($F = 72.6$, $df = 3$, $P < 0.001$). Post hoc comparisons

showed that the vigilance frequency was significantly higher in winter than during other seasons in males, but it was not significant in females (Fig. 1c). Significant differences were found among spring, summer and winter, but not autumn (Table 1).

The group size effect

Both females and males spent more time being vigilant (the percentage vigilance) in smaller groups than in larger groups in spring, summer and autumn (Table 2; Fig. 2a–c). In winter, the percentage vigilance had a negative correlation with group size in females, but not in males (Table 2; Fig. 2d).

The vigilance duration for both sexes decreased as group size increased in spring and summer, and also for females in autumn and winter (Table 2; Fig. 3a–d). However, such a correlation between vigilance duration and group size for males was not found in autumn and winter (Table 2; Fig. 3c, d).

There was a negative correlation between group size and vigilance frequency of females and males in spring, autumn and winter (Table 1; Fig. 4a–c). Such a correlation between vigilance frequency and group size was not, however, found for males in winter (Table 1; Fig. 4d).

Table 1 Statistical results from the *t* test comparing percentage vigilance, duration and frequency between sexes in each season

Season	<i>N</i>	Percentage (%)	Duration (s)	Frequency (times)
Spring	355 (F)	$t = 1.7$	$t = 1.3$	$t = 3.0$
	268 (M)	$P = 0.108$	$P = 0.001^*$	$P = 0.003^*$
Summer	390 (F)	$t = 4.1$	$t = 8.8$	$t = 5.5$
	367 (M)	$P < 0.001^*$	$P < 0.001^*$	$P < 0.001^*$
Autumn	258 (F)	$t = 0.9$	$t = 0.2$	$t = 0.1$
	241 (M)	$P = 0.926$	$P = 0.248$	$P = 0.78$
Winter	133 (F)	$t = 6.6$	$t = 9.2$	$t = 9.7$
	120 (M)	$P < 0.001^*$	$P < 0.001^*$	$P < 0.001^*$

* Significant difference

Discussion

According to our results, the level of vigilance varied with the season. On the basis of our hypothesis, goitered gazelles should have spent less time feeding in summer because of better quality forage, and more time feeding when there was a lower density of suitable food (Xia et al. 2010). Hence, they would spend more time vigilant in summer and less in winter. However, contrary to our prediction, in summer only females increased their vigilance levels, while males decreased their vigilance to almost its

Table 2 Statistical results for correlations between group size and the percentage vigilance, duration and frequency for both sexes in each season

Season	Sex	<i>N</i>	r_s	Percentage (%) <i>P</i> value	Duration (s) <i>P</i> value	Frequency (times) <i>P</i> value
Spring	F	355	-0.25	<0.001*	<0.001*	<0.001*
	M	268	-0.24	<0.001*	0.006*	<0.001*
Summer	F	390	-0.43	<0.001*	<0.001*	<0.001*
	M	367	-0.88	<0.001*	<0.001*	<0.001*
Autumn	F	258	-0.2	<0.001*	<0.001*	<0.001*
	M	241	-0.19	0.002*	0.062	0.003*
Winter	F	133	-0.1	<0.001*	<0.001*	0.018*
	M	120	0.2	0.606	0.386	0.912

* Significant difference

Fig. 2 Effect of group size on the percentage vigilance (**a** spring, **b** summer, **c** autumn, **d** winter; *filled triangles* females, *open circles* males, *continuous lines* trendline for females, *dashed lines* trendline for males)

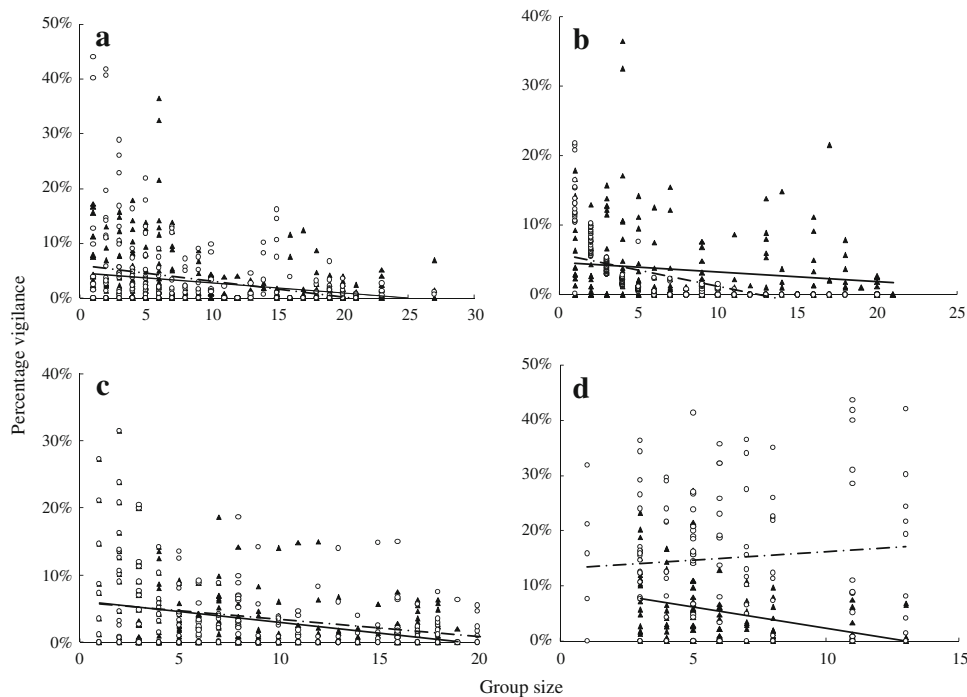
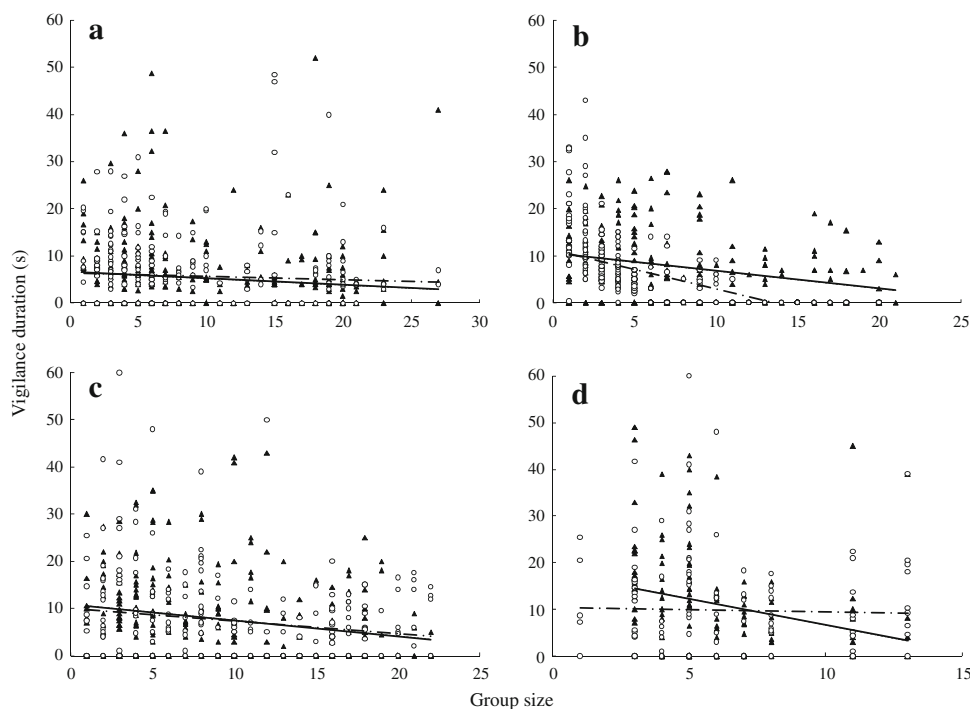


Fig. 3 Effect of group size on vigilance duration (**a** spring, **b** summer, **c** autumn, **d** winter; *filled triangles* females, *open circles* males, *continuous lines* trendline for females, *dashed lines* trendline for males)

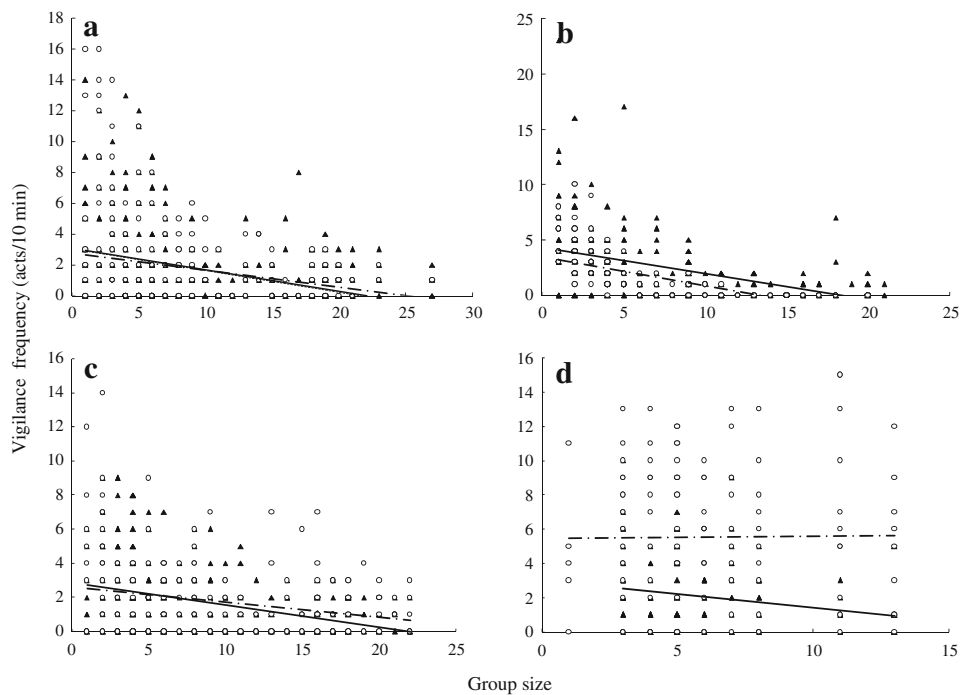


lowest level. Moreover, both females and males increased their vigilance to its highest level in winter (Fig. 1). Therefore, we concluded that the change in biomass with season did not affect the vigilance levels of goitered gazelles.

Other authors have noted considerable differences in individual vigilance levels between females and males (Childress and Lung 2003; Michelena et al. 2006; Monclus

and Rodel 2008). Some have argued that females are often more vigilant than males because males are larger and stronger, and therefore can escape from predators more easily (Clutton-Brock et al. 1982). However, during spring and autumn, we did not find any significant differences between females and males. We did find that females had a higher percentage vigilance in summer compared to males (Fig. 1), since females give birth to young during this time,

Fig. 4 Effect of group size on vigilance frequency (**a** spring, **b** summer, **c** autumn, **d** winter; filled triangles females, open circles males, continuous lines trendline for females, dashed lines trendline for males)



and mothers with young are the most vigilant among all age–sex classifications (Childress and Lung 2003; Li et al. 2009). Mothers spend extra time being vigilant to detect predators earlier and escape danger, or to hide in order to protect not only themselves but also their young.

According to our hypothesis, the vigilance level was expected to decrease during winter due to poor food quality and larger groups, but this prediction was not confirmed. Instead, males were found to be more vigilant in winter than during summer months, and more vigilant in winter than females. This contradiction is most likely attributable to the fact that males are rutting and spend more time watching out for competitors and mating partners. During the winter rut, males divide the area along the daily routes of female groups into individual ranges, known as territories. As the females pass through these territories, males usually chase them to try to keep them inside their territorial boundaries as long as possible. During this activity, the males had a much higher level of vigilance directed toward the female herds, as well as towards the movements of their male neighbors/bachelors (Blank 1998). This phenomenon was also reported for impala (*Aepyceros melampus*) (Shorrocks and Cokayne 2005) and Przewalski’s gazelle (*Procapra przewalskii*) (Li et al. 2009). Therefore, our results indicated that predation risk is not the only cause of a high level of vigilance.

In winter, female vigilance levels also increased to their highest levels across all seasons. A possible reason for this could be an anthropogenic factor, since this reserve is being used as an important winter pasture for domestic livestock. About 2,000 herdsmen and 200,000 head of

livestock (mostly sheep) arrive annually for the winter months (Chu et al. 2008; Liu et al. 2008). Our study did not include interactions between gazelles and herdsmen and their livestock; however, with the presence of domestic livestock, the wild animals might decrease their feeding durations, change their grazing times from daytime to night, or even migrate to other pasture locations. All these changes of behavior, however, would start with a considerable increase in vigilance as a result of the foreign presence around them (Childress and Lung 2003; Hochman and Kotler 2006; Manor and Saltz 2003). Moreover, since domestic herds are wintered here every year, even the absence of herdsmen and livestock may have a considerable effect on observed behavior (Canfield 1999; Cassirer et al. 1992; Tyler 1991). It is therefore suggested that anthropogenic factors may have a noticeable influence on the vigilance of goitered gazelles during winter in the Kalamaili Nature Reserve.

Many previous investigations of vigilance in ungulate species have demonstrated that an individual’s vigilance level decreases with as group size increases, because of the “group size effect” (Lima and Dill 1990; Roberts 1996; Beauchamp 2003; Shorrocks and Cokayne 2005). Our results also showed that group size has a significant effect on the vigilance levels of females and males during spring, summer and autumn (Figs. 2a–c, 3a–c, 4a–c) and females in winter (Fig. 4d). During these three seasons, gazelles had a higher degree of vigilance in smaller groups than in larger ones. This result corresponds with our hypothesis regarding the group size effect in goitered gazelles. The correlation between vigilance and group size is particularly

pronounced during the winter breeding season, although we did not find this same correlation for males in winter. Due to the social behaviors of males, vigilance levels did not vary with group size in winter (Figs. 2d, 3d, 4d). This is attributed to the fact that males spent more time searching for females and protecting their territories against rivals, increasing the vigilance levels of males.

Thus, based on our study, we found that seasonal factors do not have a considerable influence on the level of vigilance, while group size has a tangible effect on the vigilance of individual gazelles. In contrast, reproductive seasonality was a very powerful influence on the level of vigilance (for females during the birth season, and for males during the rutting season).

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