Accepted Article

The group size effect and synchronization of vigilance in Tibetan wild ass

Xinxin WANG[a,#], Le YANG[b,#], Yumeng ZHAO[a], Cong YU[a], Zhongqiu LI[a,*]

[a]School of Life Sciences, Nanjing University, 163 Xianlin Avenue, Nanjing, 210023, China; [b]Tibet Plateau Institute of Biology, 19 Beijing West Road, Lhasa, 850000, China.

*Address correspondence to Zhongqiu LI. E-mail: lizq@nju.edu.cn; [#]Xinxin Wang & Le Yang contributed equally

Abstract: Vigilance behavior is considered as an effective strategy for prey species to detect predators. An individual benefits from living in a group by reducing the time spent being vigilant without affecting the probability of detecting a predator. However, the mechanism producing a decrease in vigilance with increasing group size is unclear. Many models of vigilance assume that group members scan independently of one another. Yet in recent studies, the other two patterns of vigilance, coordination and synchronization, were reported in some species. In two summers (2018 and 2019), we studied the group size effect on vigilance and foraging of Tibetan wild ass in Chang Tang Nature Reserve of Tibet. We also tested whether individuals scan the environment independently, tend to coordinate their scans, or tend to synchronize their vigilance. The results showed that individuals decreased the time spent on vigilance with increasing group size, while increased the time spent foraging. Group members scanned the environment at the same time more frequently and there was a positive correlation between group members' behaviors, indicating that Tibetan wild asses tend to synchronize their vigilance.

Keywords: Tibetan wild ass; group size effect; synchronization of vigilance

Vigilance, i.e. scanning the surroundings, could help prey species detect potential predators and could also play a role in conspecific monitoring. The phenomenon that individuals decrease the time spent in vigilance when group size increases, i.e. group size effect, has been observed in many species (Beauchamp 2003; Beauchamp 2008). The relationship between vigilance behavior and group size has been considered an adaptive advantage of group living (Pays et al. 2007). Several mechanisms might explain this phenomenon. The many-eyes hypothesis (Caraco et al. 1980) suggests that there are progressively more eyes scanning the environment for predators when group size increases. Thus, an individual can spend less time in vigilance and more time in foraging, because it benefits from the vigilance of others. However, it is worth mentioning that an individual in a large group benefits not only from the vigilance of other group members but also from a

dilution effect (Cresswell1994; Lima1995; Roberts1996). As group size increases, the probability of each individual being attacked will decrease because there are many alternative targets in the group for the predator. Some studies also explain the group size effect by the scramble competition hypothesis (Clark and Mangel 1986; Elgar 1989; Lima et al. 1999; Beauchamp and Ruxton 2003). When foraging on scarce resources, an individual may reduce the time in vigilance unilaterally to obtain more food and increase its relative success. The best response of other group members should be to decrease their own vigilance to exploit resources just as quickly. However, other studies have also found the opposite pattern, i.e. an increase of vigilance following the increase of food competition (Fattorini et al. 2018). In fact, when more competitors are present, i.e. in larger groups, scan frequency and duration may rise due to conspecific monitoring.

Three main hypotheses have been proposed to predict the vigilance behavior that group individuals should adopt in response to the risk of being preyed upon. The first suggests that group members scan the environment independently of one another. Indeed, many earlier models of vigilance assumed that group members scan independently, predicting a negative exponential distribution of interscan durations (Pulliam 1973; Pulliam et al. 1982; Bednekoff and Lima 1998; Scannell et al. 2001). If prey individuals scan randomly and independently, the time between two consecutive vigilance events will be unpredictable. Thus, predators will be unable to predict when prey will raise their heads, and therefore will be unable to exploit this information in timing their attacks (Scannell et al. 2001). Independent scanning has been observed occasionally in nature. In wild boar *Sus scrofa*, Quenette and Gerard (1992) reported that group members scanned independently of one another.

The other two hypotheses consider that individual vigilance will be influenced by the vigilance of other group members. Coordinated vigilance suggests that, to benefit as much as possible from vigilance behavior, group members coordinate their scans in nonoverlapping bouts to avoid being vigilant when another member is already vigilant. In nature, the phenomenon has been reported in only a few species of mammals (Bednekoff 1997; Clutton-Brock et al. 1999) and birds (Mcgowan and Woolfenden 1989; Ge et al. 2011). Some studies indicated that such coordination is too costly for each individual to monitor other group members to achieve coordination (Ruxton and Roberts 1999). However, some studies suggested that coordination could occur in small groups which allow efficient sharing of detection information among group members (Rodriguez-Girones and Vasquez 2002; Fernandez-Juricic et al. 2004).

Contrary to coordination, several studies have revealed that group members scan the environment at the same time more frequently, indicating the synchronization of vigilance behavior. This phenomenon has been observed in various birds and mammals (Fernandez et al. 2003; Pays et al. 2007; Pays et al. 2007; Beauchamp,2009; Pays et al. 2012; Li et al. 2016; Podgorski et al. 2016; Evans et al. 2018). The synchronization of vigilance behavior might be caused by an external disturbance (Fernandez et al. 2003; Pays et al. 2007; Pays et al. 2007) or copying behavior (Sirot,2006; Sirot and Touzalin,2009). Some synchronization of behavior between group members may be necessary to maintain and enhance group cohesion (Keverne et al. 1978). However, the synchronization of vigilance behavior is certainly not optimal to detect predators because it would increase the time when no individual is vigilant.

We studied vigilance behavior of Tibetan wild ass *Equus kiang*. Tibetan wild ass is the only wild *Equidae* species inhabiting the Tibetan Plateau. The population of Tibetan wild ass in Tibet has been estimated to be between 37000 and 48000 (Schaller,1998). In the Chang Tang Nature Reserve, Tibetan wild ass can be easily observed which makes it an ideal species to test for the group size effect on vigilance hypothesis. In this work, we investigated the group size effect on individual vigilance and foraging and we tested whether individuals scan the environment independently of one another, tend to coordinate their scans, or tend to synchronize their vigilance behavior. If group members scan their environment

2

independently of one another, we predicted that their behaviors would be uncorrelated, and the head-up events of the different individuals would be randomly distributed through time. If group members coordinate their vigilance, we predicted collective vigilance would be higher and the head-up events would be more evenly distributed through time than expected under the independent scanning assumption. Finally, if group members tend to synchronize their vigilance, we predicted collective vigilance would be lower and the head-up events would be more clustered than expected under the independent scanning assumption (Pays et al. 2007).

Materials and Methods

Study area and animals

Our study was carried out from July 10th to 30th in 2018 and from July 1st to 25th in 2019. Study was conducted in Shuanghu County (30°41′-36°41′N, 83°52′-90°26′E), which is located in the central part of the Chang Tang Nature Reserve, Tibet. The average elevation of this area is more than 5000 m. The climate is cold and dry, the annual average temperature is -6 °C, and the average annual precipitation is 50-300 mm. The dominant vegetation type is alpine meadow and the dominant plants are *Kobresia* spp and *Stipa* spp. The main herbivores in this area are Tibetan wild ass, Tibetan antelope *Pantholops hodgsonii*, wild yak *Bos mutus*, and Tibetan gazelle *Procapra picticaudata*. The main predators are wolf *Canis lupus*, snow leopard *Uncia uncia*, lynx *Felis lynx* and Tibetan blue bear *Ursus arctos pruinosus*.

Tibetan wild ass is a group-living ungulate inhabiting the Tibetan Plateau. It lives at extremely high altitude areas and is recognized as one of the least-studied mammals in the world (Sharma et al. 2004). Mating season for Tibetan wild ass occurs from late July to the end of August. Females give birth to one offspring in summer between mid-July and mid-August every two years (Schaller 1998; St-Louis and Côté 2009). There are three group types of Tibetan wild asses: female-kids groups, bachelor groups consisting of young adult males, and solitary older males which often herd female or family groups that pass within their territory (Schaller 1998). Tibetan wild ass is often found alone or in small groups but also may form herds of several hundred individuals. Schaller (1998) observed aggregations of up to 261 individuals in the Chang Tang Nature Reserve. Among potential predators, wolf and snow leopard may occasionally prey on young and old individuals (Schaller 1998). However, we still know very little about the numbers of these predators in the study area.

Behavior Recording

Data were collected by driving along the road. To avoid duplicate sampling, the route was not repeated within three consecutive days and we did not record data when returning along the same path. No regular migration patterns among populations of Tibetan wild ass have been observed and individual activities are restricted to one area (Schaller 1998). Thus, pseudoreplication could not be avoided due to unmarked animals, but the possibility of resampling a same individual would be small. We defined a focal group as a collection of individuals all positioned within 50 m of one another (Li et al. 2009) and used a video camera (Sony HDR-CX450 with a 30x lens) to record behavioral data of Tibetan wild ass. Observations were conducted during daytime hours from 08:00 to 20:00 and the distance between observers and animals was more than 300 m. Each observation began when the observer did not influence the animals' behavior and ended when any individual

was out of sight.

We could not distinguish between males and females because they have similar body size and appearance. We recorded the date and time when an observation started, duration of observation bouts and group size for each observation. We did not record groups that included foals. We recorded a total set of 218 individuals corresponding to 43 groups. Group size ranged from 2 to 12 with an average of 5.12±0.36. Duration of focal observations ranged from 10 to 20 min with an average of 14.39 ± 0.15 min.

We recorded five behavioral states: vigilance, foraging, moving, bedding and other behaviors. An individual was considered vigilant when it did not move its feet and raised its head above horizontal, scanning the surroundings (Lian et al. 2007; Li and Jiang 2008; Li et al. 2012). Foraging was defined as food seeking or chewing with the head held below the shoulders. Moving was defined as walking or trotting with the head held above the horizontal. Bedding referred to rest and rumination while sitting on the ground. Other behaviors included activities that were not listed in the above categories, such as grooming, defecating and lactating (Childress and Lung 2003; Li and Jiang 2008). We recorded the behavior of each individual and timed it to the nearest second.

Data analysis

Individual vigilance and foraging

For each individual within each group, we calculated the proportion of time spent in vigilance and the proportion of time spent foraging, because group size is expected to mainly affects these two durations (Pulliam 1973). We also calculated the frequency of vigilance, corresponding to the number of times an individual raises its head per minute. For the assumptions of normality and homoscedasticity to be fulfilled, the three variables were arcsine square-root transformed (Wang et al. 2011). In an earlier analysis of linear mixed-effects model fitted by the restricted estimation maximum likelihood (REML), we included time of day (three levels: before 12:00, 12:00–16:00, after 16:00) as a fixed factor and group ID as a random factor but found no significant effect ($t_{41} = -0.123$, $P = 0.903$ for individual vigilance; $t_{41} = 0.813$, $P = 0.421$ for individual foraging; $t_{41} = 1.350$, $P = 0.185$ for the frequency of vigilance) and thus did not consider this factor further. Thus, in the final model, we used the linear mixed-effects model fitted by REML with group size as a covariate and group ID as a random factor. The residuals of the three variables were normally distributed by Shapiro-Wilk Test.

Collective vigilance

For each group, we calculated the proportion of time when at least one member of the group scanned the environment (i.e. collective vigilance). The observed proportion of time (P_{obs}) showed collective vigilance.

We calculated the expected proportion of time (P_{exp}) under the assumption of independent scanning by $P_{exp} = 1 - \prod_{k=1}^{n}(1 - P_k)$, where P_k is the proportion of time the individual k spent in vigilance and n is the group size (Pays et al. 2007). After a square-root transformation, the observed and expected proportions were compared with a Student's t-test for paired samples. If individuals scan independently of one another, the difference between observed and expected proportions of time would not differ statistically from 0. However, if individuals tend to coordinate their scans in non-overlapping bouts,

the difference would be significantly higher than 0. If individuals tend to synchronize their scans, the difference would be significantly less than 0.

Correlation of individual vigilance

For analysis, we transformed the original data of individuals into binary sequences (0, non-vigilance activity and 1, vigilance activity) at each second. For each group, we calculated the Pearson correlation coefficient between two binary sequences of two different individuals within the group. This coefficient was calculated for all possible pairs of group members but individuals without any vigilance over the whole period were not included. Corresponding to the original data, we simulated the expected binary sequences with the same number of 0 and 1 under the assumption of independent scanning. The simulated correlation coefficient of each group was calculated and repeated 500 times. The expected correlation coefficients were calculated as the mean of the 500 simulated correlation coefficients. The observed and expected correlation coefficients were compared by two-tailed Wilcoxon signed-rank test (Pays et al. 2007; Pays et al. 2007). If individuals tend to scan independently of one another, the observed and expected correlation coefficients would not be statistically different. If individuals tend to coordinate their vigilance, the observed correlation coefficients would be significantly lower than the expected one. If individuals tend to synchronize their vigilance, the observed correlation coefficients would be significantly higher than the expected one.

All statistical analyses were carried out with SPSS 24.0 and R language (R-3.6.3). The level of statistical significance was set at $P = 0.05$. All data were reported as mean $\pm$ SE.

Results

Individual vigilance and foraging

The mean proportion of time spent on vigilance was 0.10 ± 0.01 and the mean proportion of time spent on foraging was 0.73 ± 0.02. Linear mixed models showed that the proportion of time that an individual spent in vigilance decreased when group size increased ($t_{41} = -3.074$, $P = 0.004$, Figure 1), whereas the proportion of time spent foraging increased when group size increased ($t_{41} = 2.285$, $P = 0.028$, Figure 2).

The mean frequency of individual vigilance per minute was 0.22 ± 0.20. The group size effect was also found on the frequency of vigilance per minute for an individual. The frequency of vigilance per minute decreased with increasing group size ($t_{41} = -2.988$, P=0.005, Figure 3).

Collective vigilance

The mean observed collective vigilance of 43 groups was 0.29 ± 0.04. The difference between the observed proportion of time and the expected proportion of time under the assumption of independent scanning were statistically different from 0 (Student's t-test for paired samples: $t_{42} = -3.711$, $P = 0.001$). The observed proportion was most often less than the expected proportion (Figure 4).

5

Correlation of individual vigilance

After removing the invalid groups in which none is vigilant, a total of 41 groups were analyzed for correlation coefficient. The observed correlation coefficients between two individuals in groups, considering all possible pairs, were much higher than the expected correlation coefficients (equivalent to 0) (Wilcoxon test: $N = 287$, $Z = -5.853$, $P < 0.001$; Figure 5).

Discussion

As expected, the proportion of time that an individual spent in vigilance decreased with the increase of group size, whereas the proportion of time spent foraging increased. The frequency of vigilance also decreased with the increasing group size. The results support the model of vigilance derived from Pulliam (1973) which suggests that members benefit from grouping by reducing the time spent in individual vigilance while increasing the time spent foraging. The group size effect has been reported in other ungulates like Tibetan gazelle (Li and Jiang 2008), Przewalski's gazelle *Procapra przewalskii* (Li et al. 2009; Li et al. 2012), Père David's deer *Elaphurus davidianus* (Zheng et al. 2013) and roe deer *Capreolus capreolus* (Fattorini and Ferretti,2019).

What caused the decrease in individual vigilance with group size in Tibetan wild ass? We think that the scramble competition hypothesis is unlikely to explain this phenomenon, because there are rich food resources in our study areas for Tibetan wild ass during summer, resulting in only slight competition between them. We believe that the many-eyes hypothesis and the dilution effect might be the main reasons for the group size effect in Tibetan wild ass. In our study areas, Tibetan wild asses were under predation pressure of wolves and snow leopards. Thus, living in a group could reduce the probability of being attacked for each group member because of the increase of detection probability and dilution of predation risk assuming that large groups do not attract more predators than small ones. Besides group size, there are some other factors that affect vigilance such as sex (Li and Jiang 2008), age (van der Meer et al. 2015), and social rank (Li et al. 2012). For example, in Tibetan gazelle, male individuals are more vigilant than females (Li and Jiang 2008). In Père David's deer, the vigilance levels in all-female groups are higher than in all-male groups (Zheng et al. 2013). Sex may also have an effect on vigilance in Tibetan wild ass. However, we could not distinguish between males and females to detect which sex is more vigilant. Therefore, the effect of sex, age and other factors on vigilance needs further study in Tibetan wild ass.

We compared the observed collective vigilance with the expected collective vigilance under the assumption of independent scanning. The result showed that group members simultaneously scan the environment more frequently, indicating the synchronization phenomenon at a group level. We also calculated the correlation coefficients for vigilant behavior of all possible pairs of individuals within the group at an individual level. The result showed that there is a positive correlation between group members' behaviors, which confirmed the behavioral synchronization of individuals in vigilant and non-vigilant activities. Our results indicated that Tibetan wild asses tend to synchronize their vigilance. This phenomenon has also been found in other species such as eastern grey kangaroo *Macropus giganteus* (Pays et al. 2007) and greater rhea *Rhea americana* (Fernandez et al. 2003).

We think that the copying of neighbors is the main reason for the synchronization in Tibetan wild ass, because we did not detect any external disturbances during the focal sampling. We believe that for species under predation pressure, group

6

members may gain information about a predator by monitoring the behavior of conspecifics (via a copying strategy), facilitating escape from attacks. If an individual detects a predator, it may alert other group members by an alarm call or a sudden departure and its neighbors tend to copy the alerted initiator's vigilance behavior without having detected the predator themselves. Thus, waves of collective vigilance was triggered (Beauchamp et al. 2012). Indeed, a group member that is alerted to danger by detecting another individual's reaction to an attacking predator could escape earlier and thus increase its individual probability of survival (Lima,1995). In addition, synchronization may allow individuals to more easily reach a consensus about the best course of action when they have detected a threat (King and Cowlishaw 2007).

In conclusion, we found a significant group size effect and a synchronized vigilance pattern in Tibetan wild ass. Future studies can be undertaken on more intrinsic and extrinsic factors that might affect vigilance patterns of Tibetan wild ass, as we only focused on the group size factor in this study due to sampling difficulty.

Conflict of Interest

The authors declare that they have no conflict of interest.

Ethical approval

All applicable international, national, and institutional guidelines for the care and use of animals were followed. Under Chinese law, no specific approval was required for this noninvasive study. In addition, this study does not involve human participants.

Informed consent

All authors contributed to the study conception and design. All authors read and approved the final manuscript.

References

Beauchamp G, 2003. Group-size effects on vigilance: a search for mechanisms. *Behav Process* **63**: 141−145.

Beauchamp G, 2008. What is the magnitude of the group-size effect on vigilance? *Behav Ecol* **19**(6): 1361−1368.

Beauchamp G, 2009. Sleeping gulls monitor the vigilance behaviorof their neighbours. *Biol Letters* **5**(1): 9−11.

Beauchamp G, Alexander P, Jovani R, 2012. Consistent waves of collective vigilance in groups using public information about predation risk. *Behav Ecol* **23**(2): 368−374.

Beauchamp G, Ruxton GD, 2003. Changes in vigilance with group size under scramble competition. *Am Nat* **161**(4): 672−675.

Bednekoff PA, 1997. Mutualism among safe, selfish sentinels: A dynamic game. *Am Nat* **150**(3): 373–392.

Bednekoff PA, Lima SL, 1998. Randomness, chaos and confusion in the study of antipredator vigilance. *Trends Ecol Evol* **13**(7): 284–287.

Caraco T, Martindale S, Pulliam HR, 1980. Avian time budgets and distance to cover. *Auk* **97**(4): 872–875.

Childress M, Lung M, 2003. Predation risk, gender and the group size effect: Does elk vigilance depend upon the behaviorof conspecifics? *Anim Behav* **66**: 389–398.

Clark CW, Mangel M, 1986. The evolutionary advantages of group foraging. *Theor Popul Biol* **30**(1): 45–75.

Clutton-Brock TH, O'Riain MJ, Brotherton PNM, Gaynor D, Kansky R et al., 1999. Selfish sentinels in cooperative mammals. *Science* **284**(5420): 1640–1644.

Cresswell W, 1994. Flocking is an effective anti-predation strategy in redshanks *Tringa Tetanus*. *Anim Behav* **47**(2): 433–442.

Elgar MA, 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol Rev* **64**(1): 13–33.

Evans MHR, Lihou KL, Rands SA, 2018. Black–headed gulls synchronise their activity with their nearest neighbours. *Sci Rep* **8**: 9978.

Fattorini N, Brunetti C, Baruzzi C, Macchi E, Pagliarella MC et al., 2018. Being "hangry": Food depletion and its cascading effects on social behaviour. *Biol J Linn Soc* **125**: 640–656.

Fattorini N, Ferretti F, 2019. To scan or not to scan? Occurrence of the group-size effect in a seasonally nongregarious forager. *Ethology* **125**(5): 263–275.

Fernandez-Juricic E, Kerr B, Bednekoff PA, Stephens DW, 2004. When are two heads better than one? Visual perception and information transfer affect vigilance coordination in foraging groups. *Behav Ecol* **15**(6): 898–906.

Fernandez GJ, Capurro AF, Reboreda JC, 2003. Effect of group size on individual and collective vigilance in greater rheas. *Ethology* **109**(5): 413–425.

Ge C, Beauchamp G, Li Z, 2011. Coordination and synchronisation of anti-predation vigilance in two crane species. *Plos One* **6**(10): e26447.

Keverne EB, Leonard RA, Scruton DM, Young SK, 1978. Visual monitoring in social-groups of talapoin monkeys *Miopithecus Talapoin*. *Anim Behav* **26**(Aug): 933–944.

King AJ, Cowlishaw G, 2007. When to use social information: the advantage of large group size in individual decision making. *Biol Letters* **3**(2): 137–139.

Li C, Beauchamp G, Wang Z, Cui P, 2016. Collective vigilance in the wintering hooded crane: the role of flock size and

anthropogenic disturbances in a human-dominated landscape. *Ethology* **122**: 999–1008.

Li C, Jiang Z, Li L, Li Z, Fang H et al., 2012. Effects of reproductive status, social rank, sex and group size on vigilance patterns in Przewalski's gazelle. *PLoS ONE* **7**: e32607.

Li Z, Jiang Z, 2008. Group size effect on vigilance: Evidence from Tibetan gazelle in Upper Buha River, Qinghai-Tibet Plateau. *Behav Process* **78**(1): 25–28.

Li Z, Jiang Z, Beauchamp G, 2009. Vigilance in Przewalski's gazelle: effects of sex, predation risk and group size. *J Zool* **277**(4): 302–308.

Lian X, Zhang T, Cao Y, Su J, Thirgood S, 2007. Group size effects on foraging and vigilance in migratory Tibetan antelope. *Behav Process* **76**: 192–197.

Lima SL, 1995. Back to the basics of anti-predatory vigilance: the group-size effect. *Anim Behav* **49**: 11–20.

Lima SL, Zollner P, Bednekoff P, 1999. Predation, scramble competition, and the vigilance group size effect in dark-eyed juncos *Junco hyemalis*. *Behav Ecol Sociobiol* **46**: 110–116.

Mcgowan KJ, Woolfenden GE, 1989. A sentinel system in the Florida scrub jay. *Anim Behav* **37**: 1000–1006.

Pays O, Jarman PJ, Loisel P, Gerard JF, 2007. Coordination, independence or synchronization of individual vigilance in the eastern grey kangaroo? *Anim Behav* **73**: 595–604.

Pays O, Renaud PC, Loisel P, Petit M, Gerard JF et al., 2007. Prey synchronize their vigilant behaviorwith other group members. *P R Soc B* **274**(1615): 1287–1291.

Pays O, Sirot E, Fritz H, 2012. Collective Vigilance in the Greater Kudu: Towards a better understanding of synchronization patterns. *Ethology* **118**(1): 1–9.

Podgorski T, de Jong S, Bubnicki JW, Kuijper DPJ, Churski M et al., 2016. Drivers of synchronized vigilance in wild boar groups. *Behav Ecol* **27**(4): 1097–1103.

Pulliam HR, 1973. On the advantages of flocking. *J Theor Biol* **38**(2): 419–422.

Pulliam HR, Pyke GH, Caraco T, 1982. The scanning behavior of juncos: a game-theoretical approach. *J Theor Biol* **95**(1): 89–103.

Quenette PY, Gerard JF, 1992. From individual to collective vigilance in wild boar *Sus Scrofa*. *Can J Zool* **70**(8): 1632–1635.

Roberts G, 1996. Why individual vigilance declines as group size increases. *Anim Behav* **51**: 1077–1086.

Rodriguez-Girones MA, Vasquez RA, 2002. Evolutionary stability of vigilance coordination among social foragers. *P R Soc B* **269**(1502): 1803–1810.

Ruxton GD, Roberts G, 1999. Are vigilance sequences a consequence of intrinsic chaos or external changes? *Anim Behav*

57(2): 493–495.

Scannell J, Roberts G, Lazarus J, 2001. Prey scan at random to evade observant predators. *P R Soc B* **268**(1466): 541–547.

Schaller GB, 1998. *Wildlife of the Tibetan Steppe*. Chicago: University of Chicago Press.

Sharma BD, Clevers J, De Graaf R, Chapagaln NR, 2004. Mapping *Equus kiang* (Tibetan wild ass) habitat in Surkhang, Upper Mustang, Nepal. *Mt Res Dev* **24**(2): 149–156.

Sirot E, 2006. Social information, antipredatory vigilance and flight in bird flocks. *Anim Behav* **72**: 373–382.

Sirot E, Touzalin F, 2009. Coordination and synchronization of vigilance in groups of prey: the role of collective detection and predators' preference for stragglers. *Am Nat* **173**(1): 47–59.

St-Louis A, Côté SD, 2009. *Equus kiang* (Perissodactyla: Equidae). *Mamm Species* **835**: 1–11.

van der Meer E, Fritz H, Pays O, 2015. Anti-predator behaviorof kudu and impala in response to mimicked African wild dog presence: Do age and sex matter? *Behaviour* **152**: 1209–1228.

Wang Z, Li ZQ, Beauchamp G, Jiang ZG, 2011. Flock size and human disturbance affect vigilance of endangered red-crowned cranes *Grus japonensis*. *Biol Conserv* **144**(1): 101–105.

Zheng W, Beauchamp G, Jiang X, Li Z, Yang Q, 2013. Determinants of vigilance in a reintroduced population of Père David's deer. *Curr Zool* **59**: 265–270.

Figure captions

Figure 1. Group-size effect on the individual proportion of time spent in vigilance. Each dot represents the mean value for the group but the linear regression was calculated between group size and the proportion of time using individual values and including a 'group' random effect in the linear mixed-effects model.

Figure 2. Group-size effect on the individual proportion of time spent foraging. Each dot represents the mean value for the group but the linear regression was calculated between group size and the proportion of time spent in foraging using individual values and including a 'group' random effect in the linear mixed-effects model.

Figure 3. Group-size effect on the frequency of vigilance per minute by individuals. Each dot represents the mean value for the group but the linear regression was calculated between group size and the frequency of vigilance per minute using individual values and including a 'group' random effect in the linear mixed-effects model.

Figure 4. Difference between the observed collective proportion (P_{obs}) and the expected collective proportion of time (P_{exp}) under an assumption of independent scanning, for each observed group.

Figure 5. Difference between the observed correlation coefficient (obs) and the expected correlation coefficient (exp) under an assumption of independent scanning, for each observed group.

11

13