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Vigilance efficiency and behaviour of Bohor reedbuck *Redunca redunca* (Pallas 1767) in a savanna environment of Pendjari Biosphere Reserve (Northern Benin)

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Abstract. This study was performed to gain more knowledge about the Bohor reedbuck time budget and vigilance in a savanna habitat. Detailed data on the time-budget were collected through focal animal observation technique to determine whether the time budget activities of Bohor reedbuck was affected by vegetation cover and to test if herd size, position in herd, the age and sex affect vigilance efficiency. We fit generalized linear mixed-effect models to assess how herd size, sex, animal position in the herd and age affected individual time allocation to vigilance behaviour. The most parsimonious model averaging clearly showed how vigilance behaviour among Bohor reedbuck was strongly affected by age, sex, the total herd size and animal position in the herd accounting for the lowest Δ value of Akaike Information Criterion (AIC). Vigilance and feeding behaviour occupied the largest percent of Bohor reedbuck daylight time budget. Herd size effects were significant on different behaviour categories only when the Bohor reedbuck was observed in sympatric association. Our findings support the herd size effect hypothesis only in sympatric grouping system. However, further study is needed to investigate the possible sex-specific functions and targets of vigilance behaviour with respect to the herd direction in the field.

Key words: behaviour, herd effect, sympatric ungulate, time budget, vigilance.

Herbivore vigilance and other behaviour such as foraging, resting and moving are the result of a combination of influences from both biotic and abiotic factors (Redfern et al. 2003). It has been suggested that vigilance and foraging behaviour are mutually exclusive and produce trade-off (Randler 2005). High-level vigilance is often at the expense of other activities crucial for their maintenance (Inger et al. 2006). Therefore, animals should also balance the tradeoff between vigilance and other activities, especially foraging, resting, moving, drinking, excreting, jumping, grooming and playing (Inger et al. 2006; Benhaiem et al. 2008). As a result of this ecological shifting in time budget, animals were expected to show behavioural adaptations that reflect their immediate environments driving by vegetation height, vegetation cover, human disturbance and predation risk (Poysa 1994) as well as some intrinsic aspects such as age, sex, position in the herd and herd size (Dalerum et al. 2008; Shi et al. 2011). However, individuals grouping together may benefit from a greater number of alert eyes and prey individuals, allowing a decline in individual vigilance and increase in other behaviour categories time budget: the classical "herd-size" effect (Quenette 1990).

Many studies have identified factors affecting individual vigilance levels (Fernández-Juricic et al. 2007). It has been proposed that the free ranging antelopes such as grazers are more vigilant in open habitats than in densely vegetated areas due to better visibility and more escape space (Hopcraft et al. 2005) and deserve less time for other behaviour categories such as moving, resting and foraging. However, a recent review showed that the expected pattern of vigilance changes in relation to herd size in sympatric association are still not well understood in herd-forming species, and that field studies are required which help to reconcile isolated theories (Beauchamp 2009). This also suggests questions concerning the vigi-

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lance efficiency in sympatric association interaction of social, intrinsic factors, and other environmental effects on the anti-predator tactics of prey animals.

Within, the Reduncinae sub-family, herd size varies largely amongst species. For example the herd size of the Bohor reedbuck (*Redunca redunca*) doesn't exceed six individuals (Afework et al. 2009) compared to the waterbuck (*Kobus ellipsiprymnus*) and kob (*Kobus kob*), which can reach 35 and 65, respectively (Kingdon 1982). The three species are savanna grazers and they forage not far away from water sources (Kingdon 1982). They are mostly found in Pendjari Biosphere Reserve living in sympatric association (Kassa et al. 2007; Sinsin et al. 2008). This sympatric behaviour may be beneficial for the species having the smallest herd size such as Bohor reedbuck in increasing herd size to reduce the predation risk. Because, in animals living in herds, individual time allocation for vigilance decreases while increasing for other behabiour activities with herd size, as more eyes and ears are watching predators (the many-eyes hypothesis: Pulliam 1973); in turn, individuals in herd dilute individual risk of attack (the risk-dilution hypothesis: Foster and Treherne 1981). As a result of the ecological difference in herd size of the three sympatric bovid species, the Bohor reedbuck was expected to show different foraging behaviour categories when living in sympatric association.

Grouping has been extensively studied as a form of anti-predator behaviour in many kinds of animals, including ungulates (Fischer and Linsenmair 2006; Dalerum et al. 2008; Shi et al. 2011; Pays et al. 2012). Also, the assumption that predation risk drives changes in herd size in different habitats has been challenged in recent studies (Creel and Winnie 2005). However, the relationship between herd size, habitat type, grass height and sympatric behaviour has not been thoroughly examined for the Bohor reedbuck.

In this study, we determined how different behaviour time budget activities of Bohor reedbuck were affected by habitat types and grass height. Finally, we determined whether the herd size (including other species or not), the position in herd, the age and sex influenced the Bohor reedbuck vigilance behaviour. We predicted that the Bohor reedbuck different behaviour categories would be strongly affected by (i) their ecological environment, specifically, habitat type and grass height; (ii) in keeping with the herd-size effect, we expected that the presence of sympatric species would lead to a significant decrease in individual vigilance and, consequently, increased other foraging behaviour categories time budget because of early warning and a dilution effect. (iii) males will be more vigilant than females because they are also watching for intruding males and adults should be more vigilant than young because young have not yet learned to be sufficiently vigilant, (iv) edge animals should be more vigilant than center animals because they may be the first to encounter mammalian predators.

Methods

Study site

The Pendjari Biosphere Reserve (PBR) is situated in the north-western Benin (10°30'–11°30N; 0°50'–2°00'E, Fig. 1). It was declared a Game Reserve in 1954 and upgraded to the National Park of Pendjari (NPP) in 1961. Nowadays, it comprises a strictly protected core area (named "National Park" covering 2,660 km²) and two adjacent hunting zones named "Konkombri" and "Pendjari" hunting zones, which are on the Eastern and South-Western sides of the National Park, respectively, (covering together 1,971 km²). The PBR is limited by the foothills of the Atacora massif in the East and by the river Pendjari in the North and the West.

This reserve is under a tropical climate with a seven-month dry period during which game can be hunted by tourists. Mean annual precipitation is 1,000 mm, with most rain falling between late May and early October. The mean annual temperature is 27°C. During the rainy season, numerous small ponds in the vicinity of the large natural ones named Tiabiga, Fogou, Mondri, Diwouni, Yangouali and Bali in the centre of the National Park are full of water. During the dry season, natural ponds attract a variety of animal herds, especially large mammals searching for water. The vegetation cover of the PBR is made up of a mosaic of grasses, shrubs, trees and woodland savannas, which are burnt every year to provide fresh pasture to herbivores that dominate the reserve, to provide visibility to wildlife tourists and hunters, who visit mostly during the dry season, and to avoid uncontrolled mid or late dry season fires that spread from surrounding villages or that are lit by poachers. In the flood plains, *Mitragyna inermis*, *Panicum anabaptistum*, *Schyzachirum rupestre*, *Andropogon canaliculatus*, *Vetiveria nigritana, Andropogon* spp. and *Hyparrhenia* spp. are the most dominant. In drier areas, the main grass species found belong to the *Andropogon* and *Hyparrhenia*, whereas in wetter areas species such as *V. nigritana*, *P. anabaptistum*, *S. rupestre* and *A. canaliculatus* are found (Sokpon et al. 2001). To date,

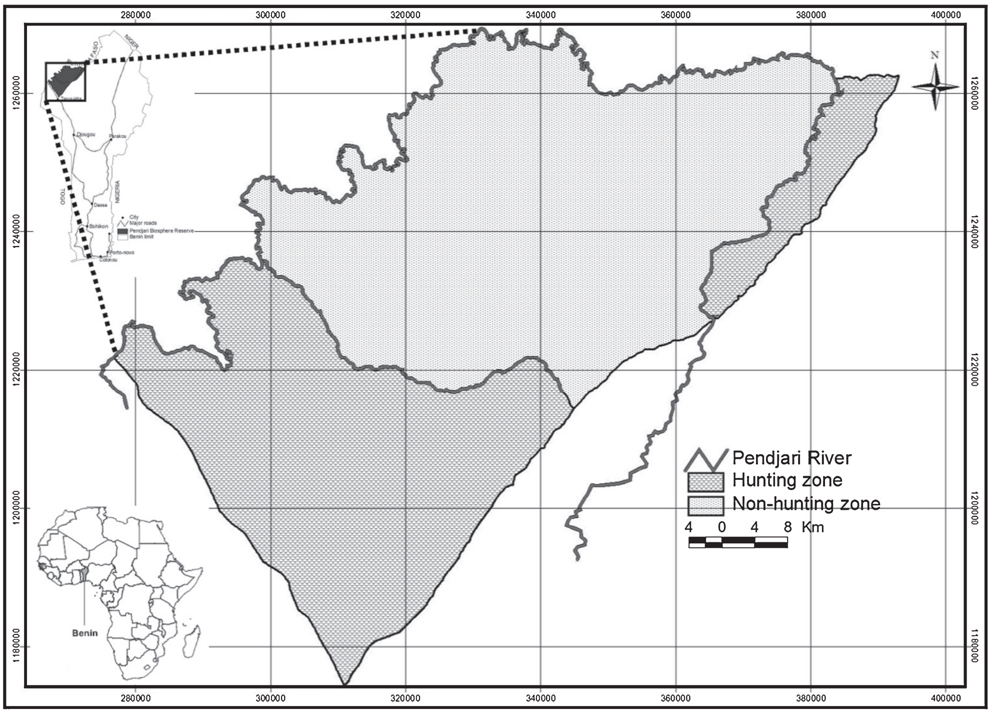

Fig. 1. Locality of Pendjari Biosphere Reserve, Benin.

only the largest mammals (Bouché et al. 2004; Di Silvestre 2008; Sinsin et al. 2008), amphibians (Nago et al. 2006), bats (Djossa et al. 2008) and some rodents (Mensah et al. 2007) living in the reserve have attracted any scientific interest. Bovid species are among the most targeted species by sport hunters throughout African savannas, particularly in Pendjari Biosphere Reserve. This reserve supports *Panthera leo* (Linnaeus, 1758), *Panthera pardus* (Linnaeus, 1758), *Acinonyx jubatus* (Schreber, 1775), *Crocuta crocuta* (Erxleben, 1777) and *Lycaon pictus* (Temminck, 1820), which can prey on Bohor reedbuck.

Data collection

Observations were made on herds of Bohor reedbuck at Pendjari Biosphere Reserve from May to July 2011 during the dry season. Data were collected along 10 line transects of 5 km each, setup along the Pendjari River due to the fact that the Bohor reedbuck live not far away from water sources in association with other species such as waterbuck and kob (Estes 1991; Kassa et al. 2007). Transects were installed at each 5 km, perpendicularly to the river in order to avoid replication in herd sampling and behaviour observation. Also to minimize the risk of non-independent samples, the behavioural data were never recorded on more than two focal animals from the same herd during the same day. Data were collected through continuous focal animal observation (Altmann 1974). All observations took place during daylight and only during active foraging time in the mornings (between 07:00–09:00h). Focal observations were conducted for 10-minute periods following Roux et al. (2009) and recorded time spent in the five behavioural categories such as feeding, vigilant, resting, moving, and other activities (e.g. drinking, excreting, jumping, grooming and playing). Antelopes were categorized as foraging when they were standing with their head below shoulder level, biting or chewing vegetation or if they were walking with their muzzle close to the ground. They were categorized as vigilant if they were standing while watching with the head at or above the shoulder level. Moving was defined as walking or running with their head at or above the shoulder level. Resting was recorded if the animal was lying down. Observations were abandoned if the focal individual moved out of view and if the herd varied in size. Data were collected on a total of 68 Bohor reedbuck herds with 135 randomly selected focal animals. The time, number of Bohor reedbuck in the herd, the number of total animals in the herd (including Bohor reedbuck), sex, age (adult, young), location in the head (edge or center), the habitat types and grass height were recorded for each observation.

Five different habitat types were distinguished: grassland (defined as open grasslands existing of tall caespitose grasses with no or rarely any trees (< 5%)), gallery forest (defined as evergreen gallery forest characterized by tall trees and no understory layer), wood savanna (defined as savannas with scarce and separated tree canopies), woodland (defined as wooded vegetation with overlapping or bordering tree canopies), outcrop vegetation (defined as vegetation located on the mountain). For grass height, a scale related to the animal's physiognomy was used: 'hoof' height when the grasses reach the hoof of the focal animal, 'knee', 'belly' and 'spine'. Female Bohor reedbucks with lambs were excluded to avoid the influence of parental care on vigilance behaviour (Li et al. 2009).

Data analysis

Accumulated time and frequency of behaviours were calculated, and each unit sampling of focal animal was used as one datum unit in statistical tests. The calculation of the time-budget was based on the total time spent on each of the behaviour elements divided by the total observation period duration (1,350 minutes). We analysed whether the each defined behaviour variable time was different among habitat types and grass height by using Analysis of Variance (ANOVA) test after checking the assumption about the normality of the data. We used Spearman's rank correlation tests to analyze the correlation between different behaviour categories applied to focal animal observed with Bohor reedbuck herd size. The factor affecting vigilance of Bohor reedbuck was assessed using the generalized linear mixed-effect models (GLMM) to highlight how the predictor variables such as herd size, sex, animal position in the herd and age affected individual time allocation to vigilance behaviour. The individual ID nested in the herd was considered as random effect while factors such as total herd size (including other sympatric species), reedbuck herd size (including only the number of reedbuck individuals recorded in the total herd size) sex, animal position in the herd (edge, centre), and age (young, adult) were used as fixed effects. In the model built, we could distinguish the "total.herd.size" as the number of individuals in the herd including other sympatric species, the "reedbuck.herd.size" including only the number of reedbuck individuals recorded in the total herd size and the "animal.position" explains the position (edge or central) of the focal animal in the herd. Model selection was conducted using a backward stepwise procedure where we used Akaike's Information Criterion (Akaike 1973) to remove parameters stepwise (factors were excluded if this improved the model fit by > 2 AIC units) and select the most parsimonious model with the best fit to the data (Bolker et al. 2008). All statistical analyses were done using R for Microsoft Windows version 2.14.2 (R Development Core Team 2012), using an alpha value of 0.05 as threshold for significance.

Results

Time budget according to habitat types and grass height

Figures 2A and 2B give an overview of the time budget proportion of the five categories of behaviour (vigilance, resting, moving, foraging and other activities) defined in this study across different habitat types and grass height, respectively. Comparison amongst habitat types for each of the five categories of behaviour show a non significant shifting in time budget devoted for vigilant behaviour (ANOVA: $F_{(4,130)} = 1.321$, $P = 0.265$), moving behaviour (ANOVA: $F_{(4,130)} = 0.672$, $P = 0.612$) and other activities (ANOVA: $F_{(4,130)} = 1.482$, $P = 0.211$).

But the time budget of Bohor reedbuck being foraging (ANOVA: $F_{(4,130)} = 2.568$, $P = 0.041$) and resting (ANOVA: $F_{(4,130)} = 8.972$, $P < 0.001$) were significantly different among habitat types. The higher values occurred in the wood savanna (36%) and woodland (33%) for the time budget of Bohor reedbuck being foraging while the largest value of being resting was recorded in gallery forest and in outcrop vegetation (31 and 17%, respectively). Non significant difference was found in the proportion of the time budget devoted by Bohor reedbuck for all the five behaviour categories investigated within the grass height classes.

Herd size effect on different behaviour categories

The herd size formed by both Bohor reedbuck and other sympatric species was found to be negatively correlated with vigilance behaviour (Spearman's rank correlation test: $r = -0.57$, $n = 135$, $P < 0.001$) while this relationship was significantly positive in foraging behaviour (Spearman's rank correlation test: $r = 0.23$, $n = 135$, $P = 0.005$) indicating that the Bohor reedbuck spent more time for foraging when herd size increased. It was also found that the duration of resting follows the same trend as foraging time and increase significantly with the herd size which, include other species (Spearman's rank correlation test: $r = 0.23$, $n = 135$, $P = 0.005$), while non-significant correlation was found between moving behaviour time duration and herd size (Spearman's rank

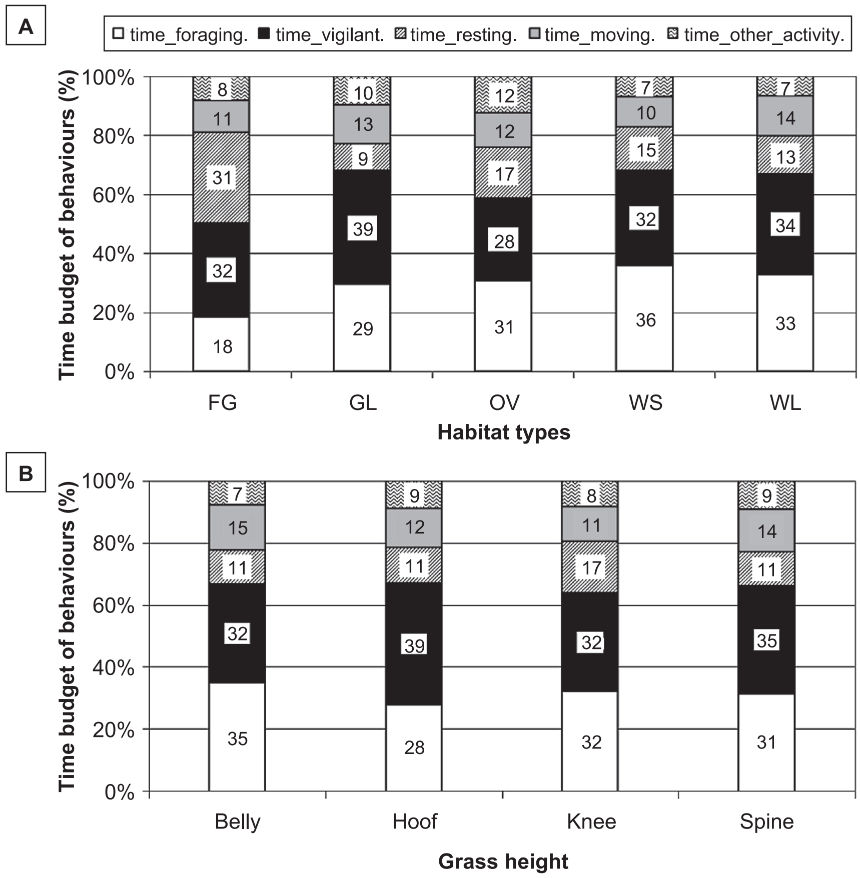

Fig. 2. Time budget of Bohor reed buck (*Redunca redunca*) according to the habitat type (A): gallery forest (GF), grassland (GL), outcrop vegetation (OV), wood savanna (WS) and woodland (WL) and glass height (B).

Table 1. Spearman correlation test investigating the correlation between different behaviour categories applied to focal animal observed and Bohor reedbuck herd size (*n* is the number of focal animals)

Behaviour	Herd size with only Bohor reedbuck				Herd size including other species			
	n	*r*	95%IC	*P*-value	*n*	*r*	95%IC	*P*-value
Vigilance duration (s)	37	–0.141	[–0.30;0.03]	0.100	135	–0.57	[–0.61;–0.36]	< 0.001
Resting duration (s)	37	0.142	[–0.02;0.30]	0.090	135	0.34	[0.19;0.48]	< 0.001
Moving duration (s)	37	–0.067	[–0.23;0.10]	0.438	135	–0.10	[–0.26;0.06]	0.240
Foraging duration (s)	37	0.095	[–0.07;0.26]	0.273	135	0.23	[0.06;0.38]	0.005
Other activities duration (s)	37	0.014	[–0.15;0.18]	0.866	135	0.08	[–0.08;0.25]	0.310

correlation test: $r = -0.10$, $n = 135$, $P = 0.24$) as well as other behaviour activities and herd size (Spearman's rank correlation test: $r = 0.08$, $n = 135$, $P = 0.31$) (Table 1). Surprisingly, no significant correlation was found between the time spent for the different behaviour categories and the herd size only formed by Bohor reedbuck.

Linear mixed model with vigilant behaviour as response variable

Among the 10 candidate generalized linear mixed models (GLMMs), only two models were retained as the most parsimonious accounting for the lowest value of ΔAIC (Table 2). However, sex, age classes, total herd size and position of the focal animal in the herd contributed to explaining more such variability, as shown, respectively, by the two top ranked selected models (ΔAIC < 2; Table 2). The most parsimonious model averaging (Table 3, top panel model in Table 2) clearly showed how vigilance behaviour among Bohor reedbuck was strongly affected by age, sex, the total herd size and

Table 2. Set of the ten most parsimonious and global generalised linear mixed model with vigilant behaviour as response variable

Model	–2LogLik	AIC	ΔAIC
total.herd.size + age + sex + animal.position + age × animal.position + total.herd.size × age + sex × animal.position	**153.5**	**168.3**	**0**
total.herd.size + age + animal.position + age × animal.position + total.herd.size × age	**154.3**	**169.5**	**1.2**
total.herd.size + reedbuck.herd.size + sex + total.herd.size × sex	151.4	171.1	2.8
total.herd.size + age + animal.position + sex + sex × animal.position + age × animal.position + total.herd.size × age	153.4	171.4	3.1
total.herd.size + age + animal.position + total.herd.size × age	160.1	172.1	3.8
total.herd.size + age + sex + sex × age + age × total.herd.size	159.5	173.5	5.2
total.herd.size + age + animal.position + sex + sex × animal.position + age × total.herd.size	159.4	175.4	7.1
total.herd.size + age + animal.position + sex + sex × animal.position + age × animal.position	160.9	176.9	8.6
total.herd.size + age + animal.position + age × animal.position + total.herd.size × age	154.1	178.1	9.8
total.herd.size + age + animal.position + age × animal.position + total.herd.size × age + sex × age	150.6	179.6	11.3

The models were ranked by the corrected Akaike Information Criterion corrected for small samples (AIC). (ΔAIC = difference in AIC between the best and the actual model; the most parsimonious model is on the top of the list)

Table 3. Estimates for the most parsimonious model of the vigilant behaviour, for further details see Table 2 (*SE*: Standard Error)

	Estimates	*SE*	*z*-value	*P*-value
intercept	2.430	0.120	20.207	< 0.001
total.herd.size	–0.036	0.004	–7.861	< 0.001
young	–0.451	0.167	–2.697	0.007
male	0.098	0.122	0.807	0.041
edge	0.150	0.139	–1.077	0.028
young × edge	0.404	0.161	2.504	0.012
total.herd.size × young	0.019	0.007	2.758	0.005
male × edge	0.049	0.155	0.321	0.748

position in the herd accounting for the lowest value of ΔAIC. From this model, the vigilance behaviour was negatively associated to the herd size (–0.036 ± 0.004) and young animal (–0.451 ± 0.167). The edge position (0.150 ± 0.139), the young animal located in the edge position (0.404 ± 0.161) and the interaction between herd size and young animal (0.019 ± 0.007) were found to increase significantly the vigilance behaviour time budget (Table 3).

Discussion

A statistically significant negative correlation between herd size and individual vigilance level was observed in this study of Bohor reedbuck. In a large herd, an individual benefits not only from the vigilance activity of the other herd members, but also from a dilution effect (Li et al. 2009). This finding is in accordance with many other previous studies in birds and mammals (Beauchamp 2008). Indeed, as individuals may benefit from both a dilution effect (i.e. the probability of any one individual being targeted by a predator decreases with herd size; Hamilton 1971), and a many-eyes effect (i.e. the chance that at least one individual in a herd is vigilant at any given moment increases with herd size; Pulliam 1973), individuals can afford to decrease their own level of vigilance in larger herds. This pattern has been reported in many taxa (Pays et al. 2007), but how individuals combine both their duration and frequency of vigilance to reduce the risk of predation is not well understood (Sirot and Pays 2011). It is also likely that larger herds may allow animals to rely on apprehensive foraging, whereas animals in smaller herds have sometimes to dedicate more time vigilance as the herd size is too small to rely on the many-eyes effect. Higher perceived risk of predation leads to increased individual vigilance in many species (Pays et al. 2007). However, the extent to which prey adjust their vigilance to the context (vegetation cover, grass height, herd size), or to a perceived risk of predation associated with the immediate presence of predators, or both, remains poorly understood. Therefore, we might except through our study that in the dense vegetation (such as gallery forest and woodland) the predation risk is higher than in the open habitat (such as grassland, wood savanna and out crop vegetation) as the probability to detect the predator reduces, and hence individuals have to devote more time for vigilance. But for the Bohor reedbuck, we found that the duration in vigilance is not statistically different according to the habitat types and grass height classes. This finding suggests that change in the vegetation pattern did not affect the vigilance behaviour of the Bohor reedbuck. While similar results have been reported in prey species

(Blumstein et al. 2003), other studies have reported that vigilance of prey may either increase (Pays et al. 2009) or decrease (Beauchamp 2010) with distance to cover. Such variability seems to be related to many factors including whether the prey perceived cover as obstructive or protective (Li et al. 2009).

The Bohor reedbuck species have to deal with a large range of potential predators in savanna ecosystems. Hence, it is not surprising that habitat type and grass height classes are not a useful proxy for predation risk in the context of the Pendjari Biosphere Reserve. Surprisingly, the time spent foraging and resting by Bohor reedbuck was influenced by the habitat types with the most time spent foraging occurring in the wood savanna and the least in the gallery forest. The gallery forest mostly used for resting could be because grass provides very little cover in gallery forest, making it advantageous to lie down when being vigilant, as standing animals are very conspicuous in open habitats. Also, due to the openness of grassland, Bohor reedbuck can still scan the surroundings when they are feeding, which is harder to do in woodland or gallery forest.

One of the fundamental assumptions underlying most vigilance models is that animals are unable to be vigilant while feeding (Pulliam et al. 1982), but the advantage of being in a herd is that it allows individuals to feed while benefiting from the vigilance of others in the herd (Pulliam et al. 1982). The results of the present study also support the prediction of "edge-effect" because individual Bohor reedbuck at the periphery of a herd was more vigilant than those in the centre, which corroborates with the findings of previous investigators (Blanchard et al. 2008). Although the lower vigilance level of central individuals may be because those individuals concentrate around a high-quality patch of gradually depleted food and increase their intake rate (Hirsch 2007). This is less likely to happen in our study because the food resources were sparsely and evenly distributed across the study area (Kassa et al. 2007). Di Blanco and Hirsch (2006) have demonstrated that the spatial position with respect to herd direction (e.g., front edge, end edge, etc.) is an important factor in determining individual vigilance level, but most of such studies (including our present one) have not measured the spatial positions with respect to the direction of the herd (Black et al. 1992), which suggest the need for further investigation.

Vigilance duration was detected to increase with male in Bohor reedbuck this could be related to the fact that males often watch for mates and competitors as well as predators. However, as has been shown for waterbuck (*Kobus ellipsiprymnus*), and kob (*Kobus kob*, Burger and Gochfeld 1994), male are often more vigilant than females, which support our findings. In the vigilance model, young Bohor reedbuck was less vigilant, confirming our initial prediction, and corroborating others results with ungulates (Boukhriss et al. 2007). But, the lowered vigilance can be partially offset by parental vigilance and by increased adult vigilance (Burger and Gochfeld 1994). The interaction of young animal and edge side was also found to increase the Bohor reedbuck vigilance duration, suggesting that the strength of the edge-side effect varies with animal age, which supports the findings by Boukhriss et al. (2007), who stated that the position in the herd independently from animal age had a significant effect on vigilance. The vigilance time budget was found to increase in the interaction of young animal and herd size. This is contradictory to the findings in literature as young animals generally lack experience and have higher nutritional needs than adults, they can be expected not only to be less vigilant than adults, but also to decrease their vigilance level by a greater extent when troupe size increases than adults do (Teichroeb and Sicotte 2012). This result could also be interpreted as a possible consequence of increasing competition for territory with herd size in sympatric living system, which constrained more stressed young Bohor reedbuck to increase their vigilance time.

In short, our study adds to the large amount of evidence demonstrating the herd-size effect on ungulate vigilance, and also adds the importance of sympatric grouping system in Bohor reedbuck behaviour and vigilance efficiency. In addition, habitat type and grass height did not affect the vigilance behaviour of the Bohor reedbuck. Our study has also shown that within-herd spatial position is an important factor to be taken into account in the study of vigilance behaviour. However, further study is needed to investigate the possible sex-specific functions and targets of vigilance behaviour and the effect of within-herd spatial position with respect to the herd direction in the field.

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