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Factors affecting vigilance in springbok: importance of vegetative cover, location in herd, and herd size

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Abstract Vigilance in vertebrates is often inversely related to group size. We present evidence that distance to bushes and location within the herd are also critical factors in vigilance in springbok (*Antidorcas marsupialis*) in Etosha National Park, Namibia, where they are the preferred prey of cheetahs (*Acinonyx jubatus*). Most springbok feed in heterospecific herds, both by grazing on grass and browsing on bushes. We studied 1245 animals; variations in vigilance (time alert) were explained by location within the herd, distance to bushes and roads, number of springbok in each herd, and gender and age. Vigilance time decreased with increasing herd size, with increasing distance to bushes and roads, and with density. Springbok on the edge of herds devoted significantly more time to vigilance than did those in other locations, and vigilance in edge animals decreased with group size. Adults were more vigilant than young, and males were more vigilant than females. Position within the herd, and distance from bushes, were the most important variables influencing vigilance. Location in the herd and gender/age affected both browsing and grazing springbok, although other factors accounted for the differences in vigilance between browsing and grazing springbok: 1) group size was not significant for browsers, but it was for grazers, and 2) distances to bushes and road were not significant for browsers, but they were for grazers. These data relate to the risk from predators and the benefits from other group members. Springbok in bushes cannot see all members of the herd, cannot derive early warning from many group members, and are more at risk from predators because the latter can hide in the bushes.

Key words Vigilance · Group size · Gender · Foraging · Antipredator

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Introduction

Animals devote time to vigilance, mainly to detect predators. However, there are other potential reasons for increased vigilance, such as watching for competitors or searching for mates (Burger and Gochfeld 1988; Alberts et al. 1996), protecting young or preventing infanticide (Burger and Gochfeld 1994; Steenbeek et al. 1999), fostering group adherence (Quenette 1990), or avoiding parasites (Mooring and Hart 1992). Moreover, vigilance may result from a combination of these pressures.

In many vertebrates, such as birds and mammals, time devoted to vigilance decreases as group size increases (Burger and Gochfeld 1988, 1993; Elgar 1989; Quenette 1990; Cords 1995; Roberts 1996). Increased group size confers benefits such as increased predator detection and a dilution effect (Hamilton 1971; Dehn 1990; Scheel 1993). Bednekoff and Lima (1998) suggested that early detection and risk-dilution effects are distinct but interact with each other, and that it may be profitable to examine the preys' probability of being targeted before or during an attack. Further, the relationship between group size and decreased vigilance on the part of group members requires that group members monitor the vigilance of others (Lima 1995), a feature seldom examined. Many other factors are related to vigilance, and to predation risk, including vegetation height and cover (Schaik et al. 1983; Lagory 1986; Poysa 1994), human disturbance (Burger and Gochfeld 1988), location in the group, gender, age (Burger and Gochfeld 1993), and a variety of other factors (Elgar 1989; Quenette 1990).

Although the relationship between group size, vigilance, and predation is difficult to document, Cresswell (1994) showed that individual redshanks (*Tringa totanus*) in larger flocks with greater overall flock vigilance were attacked less by falcons, and Steenbeek et al. (1999) suggested that vigilance increased in situations of high predation risk. For ungulates, scan rates or vigilance varied not only by group size and predation risk, but with the utility of scanning (Scheel 1993). FitzGibbon (1989) examined the relationship of vigilance in Thomson's gazelle (*Gazella thomsoni*) to the risk of being targeted for a chase by cheetahs (*Acinonyx jubatus*) by comparing the vigilance behavior of the target with its nearest neighbor. In 14 of 16 chases, the cheetah chased the gazelle that was least vigilant. The above studies suggest that vigilance would be high when there is a high risk of predation. High predation risk may be expected to occur where there are many predators, a diverse group of predators, and a paucity of prey, or where a particular species is the preferred prey or easily captured. High predation risk may also occur when vegetation cover makes stalking easier, and predator detection more difficult, although it could also make it easier for prey to hide from predators.

In this paper we examine the factors that contribute to differences in vigilance in springbok (*Antidorcas marsupialis*) in Etosha National Park in Namibia. Springbok are the preferred and primary prey of cheetahs in the park, based on behavioral observations and counts of cheetah kills (C. Grobler, personal communication), and are also taken by lions (*Panthera leo*), leopards (*Panthera pardus*), and other predators. Since they are small relative to most other potential prey, they are more vulnerable than larger species such as zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*). In East Africa, cheetahs are also the primary predators on Thomson's gazelle (Schaller 1972; FitzGibbon 1989), a closely related ungulate of similar weight. We postulated that

1. Time devoted to vigilance should decrease with increasing group size because of early warning and a dilution effect (after Hamilton 1971).
2. Males should 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 (after Burger and Gochfeld 1994, Hunter and Skinner 1998).
3. Edge animals should be more vigilant than center animals because they may be the first to encounter mammalian predators (after Prins and Iason 1989, Burger and Gochfeld 1994), and there is less dilution effect (after Hamilton 1971).
4. Animals in cover should be more vigilant than those in the open because their visibility range is less, providing less time for early warning.
5. Total group size (including other species) should be less important, and nearest neighbor distance should be more important, in explaining vigilance behavior for animals foraging in the bushes compared to those on the open plains because the bushes obscure the visibility of herdmates, and the presence of close neighbors may increase the probability of predator detection, while increasing the dilution effect.

Methods

Springbok are a rich cinnamon-brown gazelle with a white head marked by a thin black cheek stripe and forehead patch. They weigh about 37–41 kg (Estes 1991). They live in the dry arid savannah from South Africa north to southern Angola and northern Botswana, where they are the most abundant plains antelope. Today, most survive only on protected and fenced lands, such as Etosha National Park (Estes 1991). They are a gregarious, migratory, mixed grazer and browser with a fluid social organization that is adaptable to their environment (Shortridge 1934; Nowak and Paradiso 1983; Estes 1991).

We collected data in August and September 1998 in Etosha National Park in Namibia. The habitat included arid plains, areas of sparse grass intermixed with short bushes, and savannah with sparse trees (primarily *Acacia*). Etosha has a population of 13,300 springbok, 180 lions, and an unknown number of leopards, cheetahs and hyenas (C. Grobler, personal communication). Springbok either feed in monospecific herds, or with a variety of other plains ungulates.

We observed the behavior of springbok using our vehicle as a blind. Since Etosha is an attractive tourist area, the springbok were habituated to the presence of vehicles. Etosha has a very active antipoaching unit that patrols each night, so there is little illegal hunting that might affect wariness (C. Grober, personal communication). We made observations with telescopes and binoculars, and time devoted to different activities was recorded with a stopwatch. Video tapes were used to test interobserver reliability (highly correlated, $P<0.0001$). In most herds of springbok, some individuals fed, some rested, and some groomed. Some individuals in each herd we observed were feeding. There were no copulations and little evidence of courting males among the herds observed.

Upon locating a herd, we each selected a focal animal for observation, by choosing the left edge, center, or right edge of the herd, and recorded data on each individual in turn, for 30 s. Only animals that were actively feeding were observed. We avoided making observations on the same springbok by taking data on different parts of the herd and by taking data on few animals in each herd. Further, we often recorded data on different herds at the same time, thus avoiding taking data on animals in the same herd. Herds moved very slowly, and it was possible to avoid duplication. Data were taken only once on each herd. Etosha is large enough so that different herds could be easily observed.

Before the start of each observation, we recorded the time, number of springbok in the herd and the number of total animals in the herd (including springbok). For each focal animal, we recorded gender, age (adult, young), location (edge, center-edge, or center), distance to road, distance to bushes, percent of each animal visible to us (and presumably to predators), grass height (in multiples of 5 cm), and nearest neighbor distance (using body length as an indication, Burger and Gochfeld 1994). Distance to road was the perpendicular distance the animals were from the road, but we always remained far enough from them so that they did not respond to our presence, and observations were eliminated if a car came along the road and slowed down or stopped. Any animal that was not full grown was defined as young. Edge animals were defined as the outside or second animal nearest the edge, center-edge were animals that were the third or fourth in, and all other animals were considered center animals. Therefore, only edge animals occurred in herds of up to five animals, and no center animals occurred in herds of 6–25. Observation was aborted if the animal was no longer visible because it moved behind bushes.

No springbok were observed in dense bushes because we could not keep them in view for 30 s. Distance to bushes was defined as the distance to the edge of an area with many bushes (>10 in a 4 m^2 area). Distance to bushes was estimated with error of ±10%, verified from odometer readings. It was possible for a springbok to be browsing on one small bush that was located up to 10 m from a main bush area because there were a few solitary bushes scattered away from the main bushes.

During each 30 s observation we recorded time devoted to feeding (as grazing or browsing), looking up or about (vigilance), grooming, or walking. Vigilance was defined as looking with head raised (neck above horizontal), including looking overhead or around (after Cowlishaw 1997). Since we selected foraging springbok for observation, we expected them to spend most of their time foraging, but we were interested in how much foraging time they interrupted with vigilance.

Individual springbok were used as data units in all statistical tests, and because we sampled in many parts of the park, we assumed that the sample of 1245 individuals does not include significant unintended replication. The activities of individuals were fluid, and any given animal could be in different parts of the herd and could switch from grazing to browsing. Although we collected data on 1245 animals, sample sizes in individual tables may differ slightly if it was impossible to determine the gender, or if the distance to bushes was in question.

We used linear regression on log-transformed data to determine the independent variables that contributed to explaining differences in vigilance. Independent variables were group size, location in the herd, distance to the road or bushes, gender, age, percent visible, grass height, nearest neighbor distance, or time of day (PROC GLM, SAS 1985). The procedure adds the variable that contributes the most to the R^2, then adds the next variable that increases the R^2 the most, continuing until all significant variables (P=0.05) are added. Thus variables that vary colinearly are entered only if they add independently to explaining the variation. The procedure also allows for interaction variables (i.e. group size × gender). Because of the unequal sample sizes, we used Kruskal-Wallis X^2 tests to determine whether there were differences among browsers, grazers and browsers-grazers, followed by Duncan Multiple Range tests to determine which were different. We consider a browser to be any springbok that devoted any time to browsing in the sample period.

Our overall protocol for conducting behavioral studies with animals in the field was approved by the Rutgers University Animal Review Committee, and we adhered to the *Guidelines for the treatment of Animals in Research* (ABS/ASAB 1999). Our research was approved by the Ministry of Environment and Tourism of Namibia, and we had permits to work in Etosha (no. 29477).

Results

Overall, 85% of the springbok were grazing, and the rest were browsing or grazing and browsing (Table 1). Browsers were generally in or near bushes, while grazers could be far away. Similarly, browsers were often near roads, while grazers were farther away. Individual springbok that were grazing were mostly visible, since grass height was low in most of the arid lands. Those in the bushes or edges of bushes were less visible. Grazers devoted less time to vigilance, and more time to foraging than did browsers (Table 1).

Of the variation in amount of time devoted to vigilance for all springbok, 26% was accounted for by location in the herd, distance to bushes, gender and age, number of springbok in the herd, distance to road, and the interaction between distance to bushes, herd size, and visibility (Table 2). For grazing springbok, 25% of the time devoted to vigilance was explained by the same factors, except for the interaction (Table 2). Variations in

Table 1 Variations of physical factors, herd size, and behavior of springbok compared across three forage categories. Given are mean ± SE. Below means are letters indicating significant differences across rows based on Duncan Multiple Range tests. *NS* Not significant

	Browse only	Browse and graze	Graze only	Kruskal-Wallis X^2 (P)
Sample size	149	32	1,064	
Physical factors				
Distance to bush (m)	0.20±0.11 B	0.31±0.31 B	278±10.2 A	304 (0.0001)
Distance to road (m)	48.6±4.40 B	38.7±12.2 B	129±4.75 A	109 (0.0001)
Grass height (cm)	1.97±0.08 B	2.38±0.43 B	5.37±0.19 A	97.2 (0.0001)
Percent animals visible	76.9±1.07 B	69.9±3.58 C	93.6±0.40 A	276 (0.0001)
Herd size				
Number of springbok	23.9±1.58 A	15.4±2.80 B	26.8±0.81 A	6.49 (0.04)
Number in total herd	33.0±1.95 B	28.0±4.98 B	52.2±1.56 A	28.9 (0.0001)
Time devoted to (s/30 s)				
Vigilance (s)	8.55±0.59 A	6.94±0.96 A	3.88±0.18 B	85.7 (0.0001)
Foraging (s)	21.1±0.67 B	21.97±0.97 B	25.2±0.21 A	68.2 (0.0001)
Grooming (s)	0.05±0.05 A	0.16±0.16 A	0.13±0.03 A	6.81 (0.03)
Walking (s)	0.38±0.18 A	0.94±0.38 A	0.77±0.1 A	1.35 (NS)

Table 2 Factors affecting vigilance in springbok in Etosha (General linear models, PROC GLM: *NS* not significant). Dependent variable is vigilance time in seconds per 30-s observation

	Time for vigilance	Time for vigilance for grazers	Time for vigilance for browsers
Model			
F	21.23	27.09	3.26
P	0.0001	0.0001	0.001
r^2	0.26	0.25	0.22
df	10,975	10,824	7,154
Factors entering	*F*(*P*)	*F*(*P*)	*F*(*P*)
Location in herd	44.5 (0.0001)	62.6 (0.0001	10.8 (0.0001)
Distance to bush	33.01 (0.0001)	34.4 (0.0001)	NS
Number of springbok	10.1 (0.0001)	5.60 (0.02)	NS
Gender and age	6.71 (0.01)	5.13 (0.02)	3.84 (0.05)
Distance to road	3.82 (0.05)	3.76 (0.05)	NS
Distance to bushes ×herd size×visibility	3.75 (0.05)	NS	NS

Table 3 Relationship of vigilance and grazing to physical and social factors. Given are Kendall-tau correlation coefficients (*P*) *NS* Not sigificant

	Vigilance	Graze	Browse
Sample size	1245	1064	181
Distance to road	–0.19 (0.0001)	0.19 (0.0001)	NS
Distance to bush	–0.27 (0.0001)	0.25 (0.0001)	NS
Grass height	–0.12 (0.0001)	0.11 (0.0001)	NS
Percent visibility	–0.15 (0.0001)	0.14 (0.0001)	NS
Number of springbok	–0.10 (0.0001)	0.10 (0.0001)	0.22 (0.0001)
Number in total herd	–0.18 (0.0001)	0.20 (0.0001)	0.20 (0.0009)
Nearest neighbor distance	0.05 (0.02)	–0.09 (0.0001)	–0.15 (0.01)
Time of day	NS	NS	–0.09 (0.08)

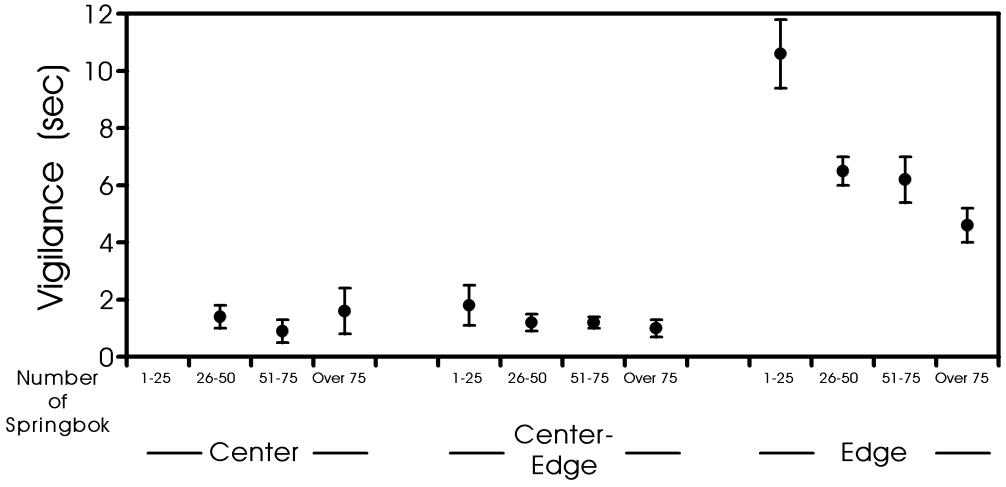

Fig. 1 Time devoted to vigilance (mean ± se, s) for springbok as a function of location within the herd and number of springbok in the herd

the time devoted to vigilance by browsing springbok, however, were explained only by location in the herd and gender and age (Table 2). Other variables, such as time of day and grass height, did not enter the models as significant variables.

Overall, vigilance behavior decreased with increasing distance from the road and bushes, grass height, percent of body visible, number of springbok in the herd, and overall herd size (Table 3). The strongest correlation was between distance to bushes and vigilance behavior. In contrast, time devoted to grazing increased as these same factors increased. However, time devoted to browsing increased only as a function of group size (springbok and total herd), and decreased with nearest neighbor distance (Table 3).

Location in the herd

Location in the herd was a significant factor affecting vigilance overall, as well as time devoted to vigilance by both grazers and browsers (Fig. 1). For all springbok, edge animals devoted significantly more time to vigilance than did center-edge or center animals, and there were no differences between center-edge and center (X^2=35.9, P<0.0001). Center animals occurred only in herds of more than 25. Although there were no consistent differences in time devoted to vigilance for center and center-edge springbok as a function of herd size, the amount of time devoted to vigilance in edge animals decreased with increasing herd size (see Fig. 1, Kruskal-Wallis X^2=21.7, P<0.0002).

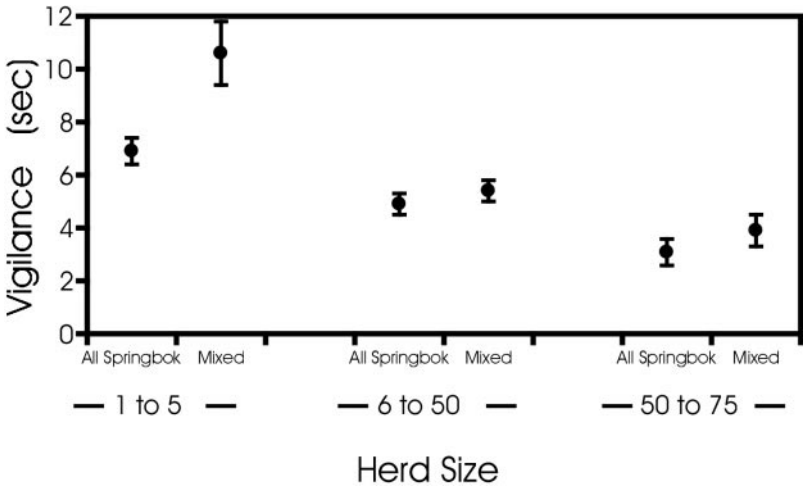

Fig. 2 Time devoted to vigilance (mean ± se, s) by springbok as a function of herd size for monospecific (all springbok) and mixed-species herds

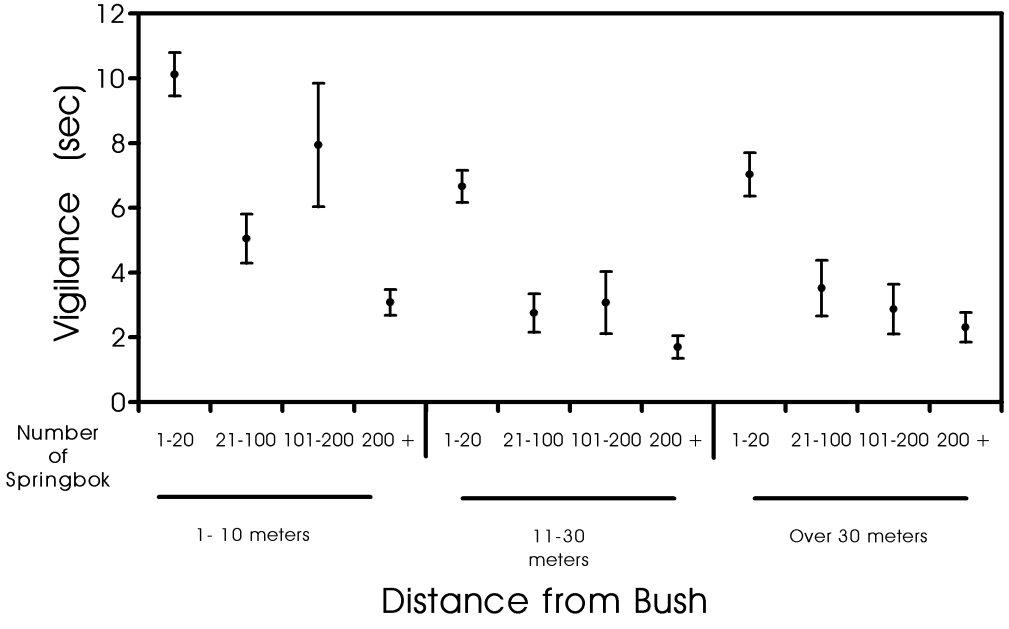

Fig. 3 Relationship between herd size and vigilance (mean ± se, s) for springbok herds that were different distances from bushes

Distance from bushes and road

Vigilance decreased with the distance from bushes, whereas time devoted to grazing increased. Overall springbok that were less than 20 m from bushes averaged 7.8±0.4 s in vigilance, whereas those farther away devoted 3.95±0.4 s or less to vigilance, and this declined to 2.5±0.2 s over 200 m (X^2=166, P<0.0001).

There were no differences in either time devoted to walking or to grooming (X^2 tests). Distance to road was less significant, although it entered the models both for all springbok and for grazers (Tables 2, 3).

Number of springbok in herds and overall herd size

Vigilance decreased with increasing group size for springbok overall. Springbok in herds of five or fewer devoted 6.9±0.5 s to vigilance, compared to 4.6±0.3 in larger herds (X^2=30.1, P<0.0001). Since vigilance decreased with increasing number of springbok in the herd, they devoted more time to grazing with increasing group size, but the relationship was not linear for browsers. Time devoted to walking and grooming did not vary by the number of springbok in a herd.

Springbok usually occurred in mixed species assemblages (79%), mainly with zebra and wildebeest. Herd size entered as a significant variable for vigilance in the overall model for springbok, but not for browsers or grazers separately (Table 2). As expected, vigilance decreased with increasing herd size, and foraging increased (X^2=67.5, P<0.0001). However, in mixed species herds, springbok devoted more time to vigilance for similar sized herds (Fig. 2). Overall herd size was significantly correlated with the number of springbok in the herd (Kendall tau=0.44, P<0.001).

Figure 3 shows the relationship between vigilance and herd size for different distances from bushes, indi-

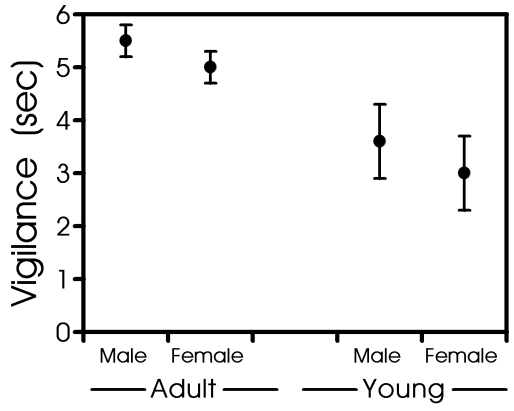

Fig. 4 Time devoted to vigilance (mean ± se, s) by springbok as a function of gender and age

cating the complexity of the relationships; vigilance generally declines with herd size for different distances from bushes.

Gender and age differences

Gender and age were significant factors in accounting for variation in time devoted to vigilance and grazing (Fig. 4). In general, adults were more vigilant than young, and males were more vigilant than females (X^2=9.5, P<0.02)). Thus, young spent more time foraging than adults, and adult females spent more time foraging than adult males (X^2=10.4, P<0.02).

Discussion

Our results indicate that time devoted to different activities varied mainly as a function of distance to bushes and the road, location in the herd, number of springbok or total animals in the herd, gender, and age (discussed below).

Location in the herd

In general, animals in the center of the herd are less vigilant than those on the edge, which has been demonstrated in several species, including Cape buffalo (*Syncerus caffer*, Prins and Iason 1989), Thomas's langurs (*Presbytis thomasi*, Steenbeek et al. 1999), and several other African ungulates (Burger and Gochfeld 1994). In this study we also found that animals on the edge were more vigilant, confirming our original prediction, but there was no difference between center-edge and center animals. This may well relate to the risk of predation; edge animals are much more vulnerable than central ones since mammalian predators must approach from the edge initially (Hamilton 1971). The relative time devoted to vigilance by edge animals is also the result of edge animals being largely in small herds. All animals in a small herd should search for predators because there are few eyes, but more importantly, should a predator begin a chase, there is little dilution effect (Dehn 1990; Scheel 1993).

Number of springbok in the herd

Herd size is usually inversely related to vigilance (Burger and Gochfeld 1988, 1993; Elgar 1989; Quenette 1990; Cords 1995; Lima 1995; Roberts 1996). Increased group size confers benefits such as increased predator detection and a dilution effect (Hamilton 1971; Dehn 1990; Scheel 1993). We suggest that increasing herd size can confer advantages only if all members of the group are visible to all members, thereby truly providing additional eyes. If, however, all members are not visible, as would be the case for animals in cover, then increasing group size may not be important.

We found that increasing group size contributed significantly to explaining time devoted to vigilance for grazers on the open, arid plains, but not for those browsing in bushes. In the latter case, springbok could not see other springbok that were hidden by bushes and would not derive direct warning advantages from them, although they might receive information through a domino effect of warning passing through the herd. Although a domino effect might operate, it would increase the time between when the first springbok noted an approaching predator, and when the last one deep in the bushes did. Thus, we suggest that increasing group size for grazers confers an early warning advantage because there are actually more eyes watching for predators, and they are visible to one another; this is less likely to be the case for springbok browsing in the bushes (see below).

Gender and age effects

Male are often more vigilant than females, as has been shown for buffalo (Prins and Iason 1989), Thomas's langurs (Steenbeek et al. 1999), and elephant (*Loxodonta africana*), zebra, wildebeest, waterbuck (*Kobus defassa*), and kob (*Kobus kob*, Burger and Gochfeld 1994). This difference seems to relate to males watching for mates and competitors as well as watching for predators. Springbok males in this study were also more wary than females, but the differences were slight.

Younger animals, especially those that are smaller and slower than adults, may be at greater risk from predators than adults. For example, FitzGibbon (1994) reported that young Thomson's gazelles that approached or inspected cheetahs were likely to be killed on 1 in 417 approaches, while for adults it was 1 in 5000 approaches.

In this study young springbok were less vigilant than adults, confirming our initial prediction, and corroborating our earlier results with other ungulates (Burger and Gochfeld 1994). FitzGibbon's (1994) observations of

greater vulnerability of young suggest that it is not adaptive for young to be less vigilant. To some extent, however, this lowered vigilance can be partially offset by parental vigilance and by increased adult vigilance (Burger and Gochfeld 1994).

Distance to road

Distance to road was a significant variable explaining variation in time devoted to vigilance for springbok overall, and for grazers. Partly this may suggest that even in a protected park they are disturbed by people, although when cars kept moving the animals looked up only momentarily. When cars stopped within about 25 m, however, most springbok (about 85%) moved away from the road before resuming foraging. Distance from the road, however, also suggests vulnerability in that we sometimes observed predators, such as lions and cheetahs, walking down roadways instead of walking through the dense bushes. In this case, however, they walk near the bushes and are not readily visible to springbok foraging in the bushes. Thus, roadways may provide an easy avenue for predators to stalk springbok that are in bushes.

Response to cover

Cover, provided by vegetation, can affect behavior in a number of ways. Time devoted to vigilance increases with vegetation height and cover, largely because it decreases the distance from which predators can be detected, and decreases the early warning time (Schaik et al. 1983; Lagory 1986). Underwood (1982) found that vigilance in ungulates was increased in thick cover, compared to sparse vegetation. However, depending upon the species, the opposite may be true; Poysa (1994) found that vigilance time among ducks increased at the greatest distances from cover, perhaps because of the small size of the birds examined, the time required for them to reach the safety of cover, the relative importance of avian predators, and the relatively large size of their mammalian predators.

Antipredator behavior can also vary by cover. Fitz-Gibbon (1994) found that Thomson's gazelles often approached and tracked predators, if they were in large groups, when there was little vegetation, or the vegetation was low. Thus, they were signaling the predators that they had been spotted, but only when the gazelles were in large groups and had good visibility. In contrast, Alberts (1994) did not find any difference in vigilance behavior as a function of cover for young baboons (*Papio cyanocephalus*). Since, as Scheel (1993) suggests, scan rates can also vary with the utility of being vigilant, small or vulnerable species might choose not to increase the time devoted to vigilance. However, springbok are fast enough to be able to evade predators, if they have sufficient warning.

Distance to bushes also reflects the distance that springboks were from cover that might hide them from predators, or provide places for predators to hide while stalking them. Vegetation cover can also make it easier for predators to stalk prey (Scheel 1993), as well as make it more difficult for members of the group to alert other members of approaching danger (Lima and Dill 1990), or to see other members that might be signaling them or fleeing from predators. Lagory (1986) examined the effect of wooded cover on behavior in white-tailed deer (*Odocoileus virginianus*) and found that deer in open pastures spent more time foraging, and less time vigilant than did deer in the forests, and deer in the wooded pasture were intermediate in behavior. Prins and Iason (1989) found that the risk of predation for buffalo was higher near the ecotone than for those that were either in dense bushes or on the open grassy plain, and the risk fell off sharply away from cover. In that case, cover provided hiding places for hunting lions. These relationships existed regardless of the amount of forage available.

The springbok in Namibia spent more time being vigilant in the bushes than in the open arid grasslands, as originally predicted. However, springbok that browsed and grazed and were generally located up to 5 m from dense bushes were less vigilant than those in the bushes. We could not make observations of springbok in extensive stands of dense bushes because they were not visible to us, and springbok mostly fed in sparse bushes with some open areas. Thus, all of our observations of springbok in the bushes could be considered ecotone. The foraging behavior of springbok in dense bushes should be examined, but the logistics of making such observations without causing disturbance are difficult.

The regression models indicated that time devoted to vigilance by grazers was generally explained by location in the herd, distance to bushes, herd size, gender and age, and distance to roads, whereas for browsers vigilance was explained only by location in the herd and gender and age (refer to Table 2). We feel that these differences relate to the risk of predation, and the probability of being warned by another springbok.

Taken altogether, our results suggest that springbok that are feeding in open grassland can make use of more of the membership of the group than can those in bushes. They can, as Lima and Dill (1990) suggest, make use of all information in their decision making about time to devote to vigilance. They can control their risk (Lima and Dill 1990) by feeding in a large group in which they can see all other individuals. Further, an animal that is in the center is surrounded by others that are more likely to be taken first by a mammalian predator (the dilution effect), and it can see other animals to take advantage of early warning. Distance to bushes may reflect how near a predator could hide while stalking them. Those that are very far from bushes are far from a stalking predator, particularly given that the grass on the arid plains is very short and predators cannot hide there. Thus, for animals in the open plains, the risk from predators is reduced by

being far from bushes, in open areas where they can see approaching predators, and monitor the warning behavior of herd members.

In contrast, springbok that are feeding in the bushes cannot see all members of the herd, particularly if the herd has more than a few animals. They cannot make use of the early warning of all other herd members in large groups because they cannot see them. Thus above a certain herd size, having more animals does not help either with early warning or a dilution effect. However, their location in the herd will make a difference, since edge animals are more at risk. For the springbok observed, the risk of predation was real, since they were the primary prey of cheetahs and were also taken by lions and other predators. Thus the springbok we observed were behaving in a manner that was consistent with assessing both the risk of predation and the potential for early detection and escape.

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References

ABS/ASAB (1999) Guidelines for the Treatment of Animals in Research. Animal Behavior Society and Association for the Study of Animal Behavior Ethical Animal Care Committee: http://www.animalbehavior.org/ABS/Handbook/abspolic99.html##treatment

Alberts SG (1994) Vigilance in young baboons: effects of habitat, age, sex, and maternal rank on glance rate. Anim Behav 47:769–755

Alberts SG, Altmann J, Wilson ML (1996) Mate guarding constrains foraging activity of male baboons. Anim Behav 51:1269–1277

Bednekoff PA, Lima SL (1998) Re-examining safety in numbers: interactions between risk dilution and collective detection depend upon predator targeting behavior. Proc R Soc Lond 263:2021–2025

Burger J, Gochfeld M (1988) Vigilance in ostrich (*Struthio camelus*): mate competition or antipredator behavior. Ostrich 59:14–20

Burger J, Gochfeld M (1993) 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 131:153–164

Cords M (1995) Predator vigilance costs of allogrooming in wild blue monkeys. Behaviour 132: 559–569

Cowlishaw G (1997) Refuge use and predation risk in a desert baboon population. Anim Behav 54:241–253

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

Dehn MM (1990) Vigilance for predators: detection and dilution effects. Behav Ecol Sociobiol 26:337–342

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

Estes RD (1991) The Behaviour guide to African mammals. University of California Press, Berkeley

FitzGibbon CD (1989) A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. Anim Behav 37:508–510

FitzGibbon CD (1994) The costs and benefits of predator inspection Behaviour in Thomson's gazelles. Behav Ecol Sociobiol 34:139–148

Hamilton WD (1971) Geometry for the selfish herd. J Theor Biol 31:295–311

Hunter LTB, Skinner JD (1998) Vigilance behaviour in Africal ungulates: the role of predation pressure. Behaviour 98:168–179

Lagory KE (1986) Habitat, group size, and the Behaviour of white-tailed deer. Behaviour 98:168–179

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

Lima SL, Dill LM (1990) Behavioural decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Mooring MS, Hart BL (1992) Animal grouping for protection from parasites: selfish herd and encounter dilution effects. Behaviour 123:174–93

Nowak RM, Paradiso JL (1983) Walker's mammals of the world. Johns Hopkins University Press, Baltimore

Poysa H (1994) Group foraging, distance to cover and vigilance in the teal, *Anas crecca*. Anim Behav 48:921–928

Prins HHT, Iason GR (1989) Dangerous lions and nonchalant buffalo. Behaviour 108:262–296

Quenette PY (1990) Functions of vigilance Behaviour in mammals: a review. Acta Ecol 11:801–818

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

SAS (Statistical Analysis Systems) (1985) SAS Users' Guide. Statistical Institute, Cary, N.C.

Schaik CPV, Noordwuk MAV, Warsono B, Sutriono E (1983) Party size and early detection of predators in Sumatran forest primates. Primates 24:211–221

Schaller GB (1972) Hunting Behaviour of the cheetah in the Serengeti National Park. East Afr Wildl J 6:95–100

Scheel D (1993) Watching for lions in the grass: the usefulness of scanning and its effects during hunts. Anim Behav 46:695–704

Shortridge GC (1934) The mammals of south-west Africa. Heinemann, London

Steenbeek R, Piek RC, van Buul M, van Hooff JARAM (1999) Vigilance in wild Thomas's langurs (*Prebytis thomasi*): the importance of infanticide risk. Behav Ecol Sociobiol 45:137–150

Underwood R (1982) Vigilance behaviour in grazing African antelopes. Behaviour 79:81–107