

Within-group spatial position and vigilance: a role also for competition? The case of impalas (*Aepyceros melampus*) with a controlled food supply

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Abstract Theory predicts that individuals at the periphery of a group should be at higher risk than their more central conspecifics since they would be the first to be encountered by an approaching terrestrial predator. As a result, it is expected that peripheral individuals display higher vigilance levels. However, the role of conspecifics in this “edge effect” may have been previously overlooked, and taking into account the possible role of within-group competition is needed. Vigilance behavior in relation to within-group spatial position was studied in impalas (*Aepyceros melampus*) feeding on standardized patches. We also controlled for food distribution in order to accurately define a “central” as opposed to a “peripheral” position. Our data clearly supported an edge

effect, with peripheral individuals spending more time vigilant than their central conspecifics. Data on social interactions suggest that it was easier for a foraging individual to defend its feeding patch with its head lowered, and that more interactions occurred at the center of the group. Together, these results indicate that central foragers may reduce their vigilance rates in response to increased competition. Disentangling how the effects of competition and predation risk contribute to the edge effect requires further investigations.

Keywords Vigilance · Food control · Edge effect · Predation · Competition

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Introduction

Theory predicts that individuals at the periphery of a group should be at higher risk than their conspecifics at the center, since they would be the first to be encountered by an approaching terrestrial predator (Hamilton 1971). As a result, it is expected that individuals increase their vigilance when at the periphery (i.e. the “edge effect”, [Inglis and Lazarus 1981]). Empirical data support both higher levels of predation (Balmford and Turyaho 1992; Lingle 2001) and higher vigilance rates (Jennings and Evans 1980; Underwood 1982; Burger and Gochfeld 1994) for individuals on the edge of a group. Accordingly, a spatial structuring of foraging groups is a common assumption in modeling of food intake and vigilance (e.g., Proctor et al. 2006).

Under field conditions, however, there are a number of limits which hinder reliable investigations of the edge effect. For instance, a higher vigilance rate among peripheral individuals can be interpreted as arising from higher predation risk (Hamilton 1971), but also as a by-product of group geometry, with central individuals

concentrated around a high-quality patch of slowly depleted food (Hirsch 2007), resulting in a higher intake rate and a lower scanning rate compared to peripheral conspecifics (see also Krause 1994). Moreover, groups in the field are not often organized in a way that facilitates precise definition of a “central” as opposed to a “peripheral” individual, and the shape of the group changes continuously, particularly for mobile groups (Frid 1997; Stankowich 2003; Mooring et al. 2004). Hence, in addition to insuring that the same food is available to all individuals irrespective of their within-group spatial position, placing controlled food in a predetermined spatial array may drive group members into a group shape that makes it easy to define spatial centrality.

In this paper, we present the results of a study carried out on wild impalas (*Aepyceros melampus*). We offered the animals a standardized type of food in patches, and controlled for food distribution. Reports of studies on foraging and vigilance which control for several parameters are widespread in the literature in several taxonomic groups (Arenz and Leger 1999; Blumstein et al. 2002; Fernández-Juricic et al. 2007). However, in ungulates, although many theoretical and field studies have provided important insights into the vigilance-foraging relationship (Underwood 1982; Berger and Cunningham 1988; Elgar 1989; Fortin et al. 2004), this kind of approach remains extremely rare (but see Berger 1991).

We expected individuals feeding at the periphery of the group to be more vigilant compared to central foragers. Since the role of conspecifics in the edge effect may have been previously overlooked (Krause 1994), we also collected data on social interactions at the feeding patches in order to

evaluate whether there was a higher level of competition at the center of the group. Under this hypothesis, central foragers would attempt to remain in contact with their feeding patch (i.e. head-down, as opposed to the head-up posture of vigilant individuals) in order to avoid losing it to competitors, and would thereby reduce their vigilance time.

Methods

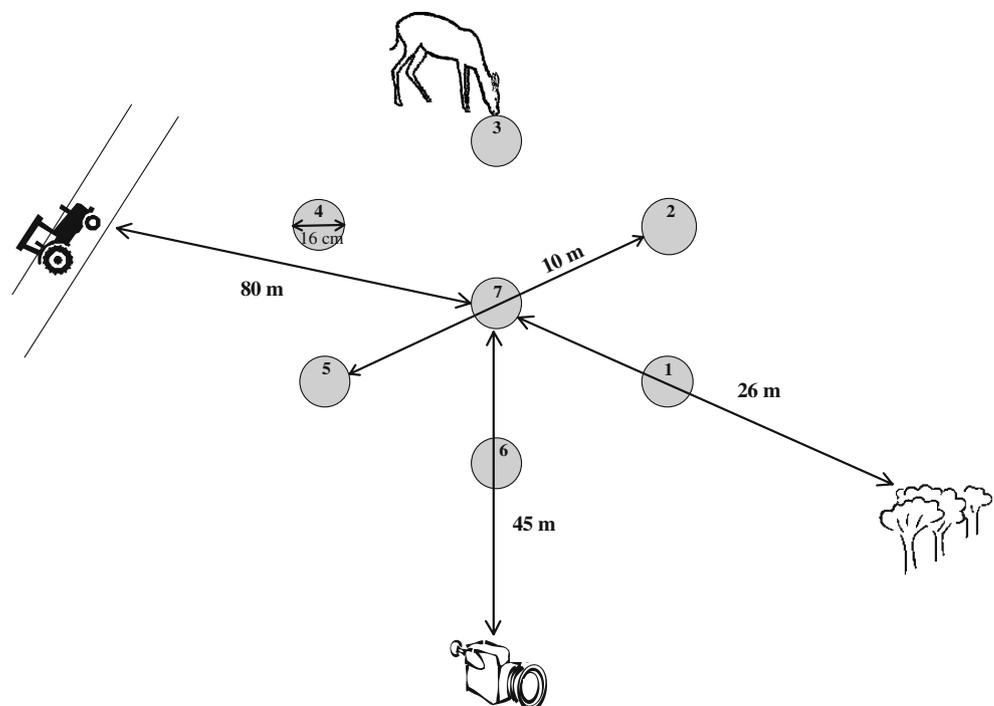
Study area

Hwange National Park is located on the North-west border of Zimbabwe (19°00'S, 26°30'E), and covers an area of ca. 15,000 km². Vegetation is typical of southern African dystrophic wooded savannas with scattered patches of grasslands. In the Main Camp region of the park, where the observations took place, impalas were mostly preyed upon by spotted hyenas *Crocuta crocuta*, hunting dogs *Lycaon pictus*, leopards *Panthera pardus*, cheetahs *Acinonyx jubatus*, and sometimes by lions *Panthera leo* (N. Drouet, A. Loveridge, G. Rasmussen, J. Salnicki, Hwange Carnivore Research Unit, pers. comm.).

Food control and behavioral observation trials

The data presented here were collected between August 5th and September 14th 2005. We collected pods fallen from umbrella thorn acacia (*Acacia tortilis*) and distributed them for the impalas in 7 patches: 6 patches were arranged

Fig. 1 Design employed in this study. Each grey circle represents about 400 g of pods collected from *Acacia tortilis*, and presented to the animals. A focal animal was considered as “peripheral” when feeding on patches 1 to 6 and “central” when feeding on patch 7



equally spaced around the circumference of a 10-m diameter circle, and the seventh was located in its center (Fig. 1). The patches were placed on sand (i.e., with no other food available), at the same places throughout all the observation trials. Each patch was made up of about 400 g of pods spread over a circle of about 16 cm diameter (ten randomly selected patches were weighed: mean weight of $404.5 \text{ g} \pm 8.3 \text{ S.D.}$).

We used a digital video camera, located 45 m away from the central patch (Fig. 1), to record vigilance behaviors. An individual was included in the analyses if the three following conditions were met for at least 29 s while it was feeding (mean observation duration: $86.1 \text{ s} \pm 55.9 \text{ S.D.}$):

- each of the seven patches was occupied by at least one animal;
- the number of individuals at the patch where the focal individual was feeding was constant;
- the total number of individuals in the group was constant.

Impalas were commonly seen running towards the pods once they had crossed a dirt road located 80 m away from the central patch (Fig. 1). We considered this distance as the limit below which an animal was considered as being part of the group.

Data collection

We performed 13 independent observation trials. We observed a mean of 6.2 individuals per trial (range 2–9), and recorded 81 focal individuals in total.

For each focal individual, we recorded the proportion of time spent vigilant during a feeding bout. An animal was considered as being vigilant when it lifted its head from the patch and scanned its surroundings. We further recorded:

- its position (center versus periphery, see Fig. 1);
- its sex (males have horns whereas females do not);
- its age (adult versus juvenile—i.e., young born 9 months previously, smaller than adults);
- the group size (range 7–39);
- the number of individuals feeding at the focal patch (1 or 2; numbers greater than 2 proved impossible to record reliably).

Individuals were not captured or marked as part of this study. Since the impalas were not individually recognizable, we may have sampled the same animals several times. However, as we were able to identify the animals within each trial by monitoring them on film, the animals were not sampled more than once during a given trial. Moreover, we included “trial number” as a random factor in the analysis, in order to control for potential non-independence between observations (on different individuals) recorded during the same trials (see “Data analysis”). Therefore, we assumed that

observations of the same animal under different conditions, if it occurred, are not an issue in our reasoning and bear little weight on the conclusions drawn from the statistical analyses.

Five individuals used both the edge and the central position within the same focal trial. This gave us the valuable opportunity to investigate the edge effect from an intra-individual perspective, in a separate analysis.

Social interactions

In order to investigate our alternative hypothesis to explain the edge effect (higher probability of losing a patch to a competitor while scanning with increased competition at the center of the group) we recorded all visible agonistic interactions at feeding patches. Because of the low number of interactions both among and between age-sex classes and because of the clear effect of age and sex on the probability of winning an interaction (adult males were dominant over all other classes, followed by juvenile males, adult females and juvenile females, from our own data), we restricted our analyses of social interactions to juvenile males ($n=37$ interactions, compared to $n=9$ for adult males, $n=5$ for adult females and $n=10$ for juvenile females). We defined “interaction” as the situation in which an animal (the “challenger”) arrived on a patch already occupied (by the “resident”), with only one of the two individuals remaining on the patch after the encounter. A challenger initiating an interaction displayed a typical aggressive behavior (with physical contact, $n=9$ —or not, $n=28$), such as horn threat display, rush threat and/or back arching. An individual (the resident or the challenger) losing the interaction usually displayed typical submissive behaviors, such as quickly moving away from the opponent.

We recorded the resident’s head posture before the interaction (head up or head down) and the outcome of the interaction (remains on or vacates the patch it was feeding on). We also recorded whether the interactions occurred at the central patch or at one of the peripheral patches in order to test whether more interactions occurred in the middle of the group.

Data analysis

We used linear mixed models (Pinheiro and Bates 2000) to investigate the effects of within-group position (center versus periphery), age, sex, group size, and number of individuals at the focal patch on the proportion of time spent vigilant (transformed using the arcsine of the square root). We included the trial number as a random factor in order to control for potential non-independence between observations recorded during the same trials. We did not include all the predictors and their interactions in a single model given the sample size. We therefore chose to

investigate the effect of the number of individuals at the focal patch in separate analyses (also including within-group position), and thus to consider all the variables classically reported to affect vigilance patterns in a single and separate analysis: within-group position, age, sex, and group size. All variables were considered as factors except group size (covariate).

We selected the model by testing the effect of the four two-way interactions by successively withdrawing each interaction and testing the difference in log-likelihood between both models (with and without each interaction) following a backward procedure. We then removed all the non-significant interactions and tested the effects of the main factors following the same procedure, while retaining the significant interaction in the model.

A potential confusion in the interpretation of the results may arise because of a polarity in the design: the animals may be more vigilant on one side of the group because of the surroundings, irrespective to their position relative to the group. Hence, for example, if animals foraging on patches 1, 5, 6, and 7 (Fig. 1) are more vigilant because of observer presence, grouping all the peripheral patches in a single category may result in an erroneous conclusion of support for an edge effect. Therefore, we also checked for any peripheral patch identity effect on vigilance behavior. We also used linear mixed models with trial number as a random factor.

We used a nonparametric Wilcoxon test for paired samples to investigate the effect of within-group position on the proportion of time spent vigilant from an intra-individual perspective, using the five animals that fed both at the center and at the periphery of the group in a given trial.

We finally considered social interactions. We used Chi-square tests to check whether a similar proportion of interactions was lost when the resident had its' head up or down, and to look at the distribution of interactions in relation to the location of the patch.

All tests are two-tailed. Biological values are given \pm one standard deviation. Two software packages were used for the transcriptions of the recorded behaviors: Pixela Image Mixer Version 1.0 for Sony and Microsoft Windows Movie Maker. All statistical analyses were performed with R software (R Development Core Team 2005).

Results

Vigilance behavior

Impalas spent more time being vigilant when feeding at the edge of the group, and this was more pronounced for juveniles compared to adults (Table 1, Fig. 2). Neither

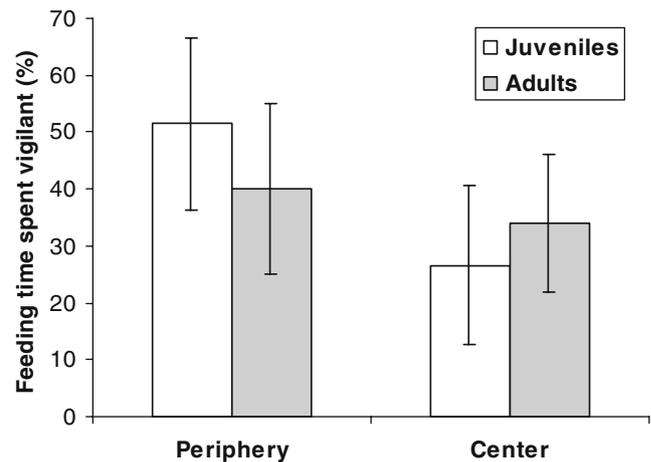


Fig. 2 The proportion of time spent vigilant by impalas while feeding, in relation to the age of the focal individual and its position within the group. See Table 1 for model selection

group size nor sex influenced the time spent vigilant (groups from 7 to 9 individuals: $71.7\% \pm 15.9$; groups from 18 to 39 individuals: $67.1\% \pm 20.5$; males: $70.9\% \pm 18.1$, females: $68.9\% \pm 14.4$; Table 1). The number of individuals feeding at the focal patch did not significantly affect the proportion of time spent vigilant (numbers at a given patch \times within-group position: L ratio=0.52, difference in $df = 1$, $p = 0.47$; numbers at a given patch: L ratio = 0.21, difference in $df=1$, $p=0.65$).

When focusing on peripheral patches only, patch identity had no effect on the proportion of time spent vigilant (L ratio=7.54, difference in $df=5$, $p=0.18$). Therefore, the effect of within-group position on the proportion of time devoted to vigilance was probably better explained by a real edge effect rather than by polarity within the experimental area.

In all five cases where the same animals were observed feeding both at the edge and at the center of the group, focal impalas were more vigilant when feeding at the periphery ($Z=-2,023$, $p=0.043$, Wilcoxon test for paired samples). On average, the five animals spent 47% (± 15.3) of their time vigilant when feeding on the edge of the group compared to 28% (± 12.4) when feeding on the central patch.

Social interactions

The outcome of an interaction at a feeding patch varied in relation to the resident's head posture before the interaction. When its head was up before the interaction, a resident was equally likely to either vacate the patch or win the interaction and resume feeding (8 and 9 cases out of 17 respectively; $\chi^2=0.06$, $df=1$, $p=0.81$). When the resident had its' head down when the challenger initiated the interaction, the resident left its patch in only four cases

Table 1 Model selection for the proportion of time impalas spent vigilant while feeding, following a backward procedure (with successive withdrawal of terms)

Model	Log-likelihood	df	Models compared	L. ratio	Difference in df	p value
(1) Vig=Tri+Grp+Sex+Age+Pos+Grp * Age+Grp * Pos+Sex * Age+Age * Pos	41.66	60				
(2): (1)—Grp * Age	40.86	61	(2) and (1)	1.60	1	0.21
(3): (1)—Grp * Pos	40.72	61	(3) and (1)	1.88	1	0.17
(4): (1)—Sex * Age	41.59	61	(4) and (1)	0.14	1	0.71
(5): (1)—Age * Pos	38.71	61	(5) and (1)	5.90	1	0.01
(6): (1)—Grp * Age—Grp * Pos—Sex * Age	39.91	63				
(7): (6)—Grp	39.68	64	(7) and (6)	0.47	1	0.49
(8): (6)—Sex	38.96	64	(8) and (6)	1.91	1	0.17
(9): (6)—Age * Pos	37.95	64	(9) and (6)	3.92	1	0.048
Selected model: Vig=Tri+Age ($p<0.05$)+Pos ($p<0.001$)+Age * Pos ($p<0.05$)						

Vig refers to the arcsine of the square root of the proportion of time spent vigilant while feeding. Tri refers to the trial number, fitted as a random term; Grp refers to the number of individuals in the group; Sex refers to the gender of the focal individual; Age refers to its age (adult or juvenile); Pos to its position in the group (center or periphery). Asterisk indicates an interaction between factors. All variables were defined as factors, except for “Grp”, defined as a covariate. P values for the final model were computed using F statistics. See also Fig. 2

out of 20 (and thus the challenger failed in 16 cases out of 20; $\chi^2=7.2$, $df=1$, $p=0.007$).

Finally, we looked at the spatial distribution of the interactions recorded during our trials, in relation to the locality of the patch. The mean number was 25.4 interactions per patch, whereas the maximum of 46 interactions occurred in the central patch ($\chi^2=44$, $df=6$, $p<0.001$).

Discussion

Our data clearly supported the prediction of an edge effect in impalas, a social species experiencing high levels of predation. Peripheral individuals spent more time vigilant compared to those feeding at the center of the group. This pattern was also clear from an intra-individual perspective, as vigilance levels increased when an individual moved from the center to the edge of the herd. Our design allowed us to control for several potential sources of bias besides food characteristics and distribution, such as distance to observer and habitat characteristics (Blumstein and Daniel 2003), as we observed stationary feeding groups from the same location. On the other hand, a weakness of our study is that there is only a single central position. However, the fact that “patch identity” did not affect our results for edge effect may suggest this is not a major problem.

Vigilance behavior has typically been investigated in the context of predation pressure. When foraging together, however, intra-group competition may constrain individuals to increase their effort “both in searching and feeding, in order to obtain their share of the available forage” (Clark and Mangel 1986). Therefore, because increased feeding effort may result in lowered level of vigilance, the decrease

of individual vigilance with increasing group size, often interpreted as a consequence of the presence of more eyes available to detect an approaching predator (Pulliam 1973), might also be the result of intra-group competition (Beauchamp 2003): more eyes implies more mouths. Similarly, Krause (1994) proposed to explain the edge effect by a higher level of competition for food in the center of the group compared to the edge, implying a decrease in scanning rate. Our data on interactions at feeding patches suggest that two conditions were met for explaining the edge effect in terms of competition: because raising the head could increase the probability of losing its patch (and not only decrease its share), a forager may reduce scanning where intra-group competition is highest, i.e., at the center of the group. In order to understand why retaining a patch appears easier with the head down, we also observed agonistic interactions in the field. In every case ($n=16$), the individual who initiated the interaction did it with its head lowered (in 10 cases, it had its head raised just before the interaction, but lowered it before the initiation). Each time the “resident” fought (i.e., eight cases out of 16; it fled in the other eight cases) it did so with its head down although its head was raised prior to the interaction in all cases. Hence, because agonistic interactions in natural conditions are probably mostly performed with head lowered, the resident in our trials was already in the optimal natural position to defend its patch when feeding on it, i.e., with its head down. Further, being on the patch probably created a “buffer effect” preventing other individuals to enter it (as in Zwartz 1976).

Since we controlled for food characteristics, including its distribution, the increased level of competition at the center of the group was not the result of the animals congregating around a high-quality patch of food (Hirsch 2007). This was

instead probably better explained by more movements—and thus encounters—at the center of the group because of (1) a higher probability of passing through the central patch when moving directly from one patch to another and (2) animals being more inclined to be attracted by the center of the foraging group because of safety reasons (Ron et al. 1996), and/or because food items as acacia pods are naturally found in well delimited places (i.e., under trees). In addition to these hypotheses explaining the higher level of actual competition in the center of the group, we suggest that the assessment of competition pressure is also probably higher for central individuals since they are surrounded by conspecifics.

The edge effect we report could thus be the result of both lower predation threat and higher competition in the middle of the group: individuals should increase their level of vigilance because of predation risk when at the periphery of the group, and decrease it because of competition pressure when at the center of the group. This hypothesis could also help us to clarify why the edge effect was more pronounced for juveniles (Fig. 2). Unlike neonates that have not yet learned to be sufficiently vigilant (Burger et al. 2000), recently independent animals may be highly reactive to all kind of stimuli, coming from both outside the herd (i.e., predatory threat, thereby strongly increasing vigilance level when feeding at the periphery) and inside the herd (i.e., social threat, thereby strongly decreasing head-up postures level when at the center of the group).

Clearly, disentangling the effects of competition and predation on vigilance levels requires further investigation. Future experimental studies could vary the level of feeding competition [e.g., the amount of food per patch, the number of patches or the distance between patches (and thus between neighbors, Fernández-Juricic et al. 2007)], or vary the risk of predation by changing the distance between the patches and cover.

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References

- Arenz CL, Leger DW (1999) Thirteen-lined ground squirrel (*Sciuridae: Spermophilus tridecemlineatus*) antipredator vigilance decreases as vigilance cost increases. *Anim Behav* 57:97–103
- Balmford A, Turyaho M (1992) Predation risk and lek-breeding in Uganda kob. *Anim Behav* 44:117–127
- Beauchamp G (2003) Group-size effects on vigilance: a search for mechanisms. *Behav Proc* 63:111–121
- Berger J (1991) Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. *Anim Behav* 41:61–77
- Berger J, Cunningham C (1988) Size-related effects on search times in North American grassland female ungulates. *Ecology* 69:177–183
- Blumstein DT, Daniel JC (2003) Red kangaroos (*Macropus rufus*) receive an antipredator benefit from aggregation. *Acta Ethol* 5:95–99
- Blumstein DT, Daniel JC, Ardron JG, Evans CS (2002) Does feeding competition influence tammar wallaby time allocation? *Ethology* 108:937–945
- Burger J, Gochfeld M (1994) Vigilance in African mammals: differences among mothers, other females, and males. *Behaviour* 131:153–169
- Burger J, Safina C, Gochfeld M (2000) Factors affecting vigilance in springbok: importance of vegetative cover, location in herd, and herd size. *Acta Ethol* 2:97–104
- Clark CW, Mangel M (1986) The evolutionary advantages of group foraging. *Theor Pop Biol* 30:45–75
- Elgar MA (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol Rev* 64:13–33
- Fernández-Juricic E, Beauchamp G, Bastain B (2007) Group-size and distance-to-neighbour effects on feeding and vigilance in brown-headed cowbirds. *Anim Behav* 73:771–778
- Fortin D, Boyce MS, Merrill EH, Fryxell JM (2004) Foraging costs of vigilance in large mammalian herbivores. *Oikos* 107:172–180
- Frid A (1997) Vigilance by female Dall's sheep: interactions between predation risk factors. *Anim Behav* 53:799–808
- Hamilton WD (1971) Geometry of the selfish herd. *J Theor Biol* 31:295–311
- Hirsch BT (2007) Costs and benefits of within-group spatial position: a feeding competition model. *Quart Rev Biol* 82:9–27
- Inglis IR, Lazarus J (1981) Vigilance and flock size in brent geese: the edge effect. *Z Tierpsychol* 57:193–200
- Jennings T, Evans SM (1980) Influence of position in the flock and flock size on vigilance in the starling *Sturnus vulgaris*. *Anim Behav* 28:634–635
- Krause J (1994) Differential fitness returns in relation to spatial position in groups. *Biol Rev* 69:187–206
- Lingle S (2001) Anti-predator strategies and grouping patterns in white-tailed deer and mule deer. *Ethology* 107:295–314
- Mooring MS, Fitzpatrick TA, Nishihira TT, Reisig DD (2004) Vigilance, predation risk, and the Allee effect in desert Bighorn Sheep. *J Wildl Manage* 68:519–532
- Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Springer, New York
- Proctor CJ, Broom M, Ruxton GD (2006) Antipredator vigilance in birds: modelling the "edge" effect. *Math Biosc* 199:76–96
- Pulliam HR (1973) On the advantages of flocking. *J Theor Biol* 38:419–422
- R Development Core Team (2005) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. URL <http://www.R-project.org>.
- Ron T, Henzi SP, Motro U (1996) Do female chacma baboons compete for a safe spatial position in a southern woodland habitat? *Behaviour* 133:475–490
- Stankowich T (2003) Marginal predation methodologies and the importance of predator preferences. *Anim Behav* 66:589–599
- Underwood R (1982) Vigilance behaviour in grazing African antelopes. *Behaviour* 79:81–107
- Zwarts L (1976) Density-related processes in feeding dispersion and feeding activity of Teal (*Anas crecca*). *Ardea* 64:192–209