

Detecting predators and locating competitors while foraging: an experimental study of a medium-sized herbivore in an African savanna

Olivier Pays · Pierrick Blanchard · Marion Valeix · Simon Chamaillé-Jammes · Patrick Duncan · Stéphanie Périquet · Marion Lombard · Gugulethu Ncube · Tawanda Tarakini · Edwin Makuwe · Hervé Fritz

Received: 12 April 2011 / Accepted: 26 November 2011 / Published online: 27 December 2011
© Springer-Verlag 2011

Abstract Vigilance allows individuals to escape from predators, but it also reduces time for other activities which determine fitness, in particular resource acquisition. The principles determining how prey trade time between the detection of predators and food acquisition are not fully understood, particularly in herbivores because of many potential confounding factors (such as group size), and the

ability of these animals to be vigilant while handling food. We designed a fertilization experiment to manipulate the quality of resources, and compared awareness (distinguishing apprehensive foraging and vigilance) of wild impalas (*Aepyceros melampus*) foraging on patches of different grass height and quality in a wilderness area with a full community of predators. While handling food, these animals can allocate time to other functions. The impalas were aware of their environment less often when on good food patches and when the grass was short. The animals spent more time in apprehensive foraging when grass was tall, and no other variable affected apprehensive behavior. The probability of exhibiting a vigilance posture decreased with group size. The interaction between grass height and patch enrichment also affected the time spent in vigilance, suggesting that resource quality was the main driver when visibility is good, and the risk of predation the main driver when the risk is high. We discuss various possible mechanisms underlying the perception of predation risk: foraging strategy, opportunities for scrounging, and inter-individual interference. Overall, this experiment shows that improving patch quality modifies the trade-off between vigilance and foraging in favor of feeding, but vigilance remains ultimately driven by the visibility of predators by foragers within their feeding patches.

Communicated by Chris Whelan.

O. Pays (✉)
LEESA, Groupe Ecologie et Conservation, Université d'Angers,
Campus Belle Beille, 2 Bd Lavoisier, 49045 Angers, France
e-mail: olivier.pays@univ-angers.fr

P. Blanchard
Laboratoire Evolution et Diversité Biologique, CNRS, ENFA,
UMR 5174, Université de Toulouse, 118 Route de Narbonne,
31062 Toulouse, France

M. Valeix · S. Périquet · H. Fritz
Laboratoire de Biométrie et Biologie Evolutive, UMR-CNRS
5558, Université Claude Bernard Lyon 1, Bât Gregor Mendel,
43 Boulevard du 11 Novembre 1918, 69622 Villeurbanne Cedex,
France

S. Chamaillé-Jammes
Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175,
CNRS, 1919 route de Mende, 34293 Montpellier Cedex 5,
France

P. Duncan
Centre d'Etudes Biologiques de Chizé, CNRS-UPR 1934,
79360 Beauvoir-sur-Niort, France

M. Lombard · G. Ncube · T. Tarakini · H. Fritz
CNRS HERD Program, Hwange LTER, Hwange Main Camp
Research, Hwange NP, Box 62, Dete, Zimbabwe

E. Makuwe
Hwange National Park, P. Bag 5778, Dete, Zimbabwe

Keywords Anti-predator behavior · Group living · Impala · Patch quality · Vigilance · Visibility

Introduction

Vigilance behavior lies at the heart of a trade-off between feeding and safety (Brown 1999). In particular, animals balance the time spent in the acquisition of resources and in

gaining information—about resources, the animals' social environments, thus feeding competition, and predators. Many studies have identified factors affecting individual vigilance levels (McNamara and Houston 1986; Lung and Childress 2006; Roth et al. 2006; Fernández-Juricic et al. 2007). However, a recent review showed that the interactive effects of food density, predation risk, and intra-group competition on the costs and benefits of vigilance are still not well understood in group-forming species, and that field studies are required which help to reconcile isolated theories (Beauchamp 2009). For instance, a negative relationship between vigilance and food density may be expected on the basis of the time-constraint on foraging that animals commonly experience (McNamara and Houston 1992; Ale and Brown 2007). In group-forming species, the need for individuals to monitor other group members, potential competitors, in order to obtain information on rich patches when food density is low may also lead to a negative relationship between food density and individual vigilance levels, even in the absence of predation (Barnard and Sibly 1981; Giraldeau and Beauchamp 1999; Beauchamp 2008). Levels of this social vigilance can increase with group size as more group members need to be monitored (Favreau et al. 2010). Under the risk of predation, the above considerations on social vigilance apply but may interact with the positive effect of group size on the likelihood of predator detection (many-eyes effect; Lazarus 1979; Lima 1995), thus leading to lower individual vigilance levels. There is, therefore, a need for studies which manipulate the factors driving individual vigilance levels (food density, predation risk, and group size).

The level of apprehension while foraging is one key factor mediating the predation risk experienced by prey. Apprehension can be defined as a reduction in attention devoted to performing an activity (foraging) as a consequence of reallocating attention to detecting or responding to predators or competitors (Dall et al. 2001; Kotler et al. 2002, 2004, 2010; Raveh et al. 2011). Apprehensive foraging allows a forager to harvest (or handle) food while increasing its alertness to predators. It is now clear that prey can often spend time vigilant while foraging, as in birds handling seeds (Popp 1988; Baker et al. 2011) and mammals chewing with their heads up (Fortin et al. 2004; Makowska and Kramer 2007). Food intake in mammalian herbivores at short time scales is generally limited by chewing and swallowing rates rather than by the encounter rate of food, and these animals can spend as much as 50% of their time scanning without reducing their food intake (Illius and FitzGibbon 1994). Thus, part or all of the time spent chewing can be used for vigilance oriented towards social monitoring or predator detection (called 'routine vigilance' in Blanchard and Fritz 2007). Here, we will distinguish two forms of awareness (i.e. time allocated to

scan the environment): apprehensive foraging when the individual is monitoring its surroundings while chewing; and vigilance, which is characterized by a marked (intense) posture of alertness. Vigilance represents the most costly form of time allocation as it disrupts the ingestion process. Indeed, animals may stop chewing as this may impair hearing. In contrast, apprehensive foraging can be considered a low cost form of awareness, since the ingestion process can continue, though the quality of information on predators may be reduced (Hochman and Kotler 2007).

Apprehensive foraging may increase with plant biomass, since bite size and the frequency of acceptable bites increase, and with them, time spent handling food. Thus, herbivores have the opportunity to allocate time to anti-predator vigilance while chewing the current bite, particularly when they are foraging on patches of high grass biomass (Fortin et al. 2004), or more generally when foraging on patches of high resource abundance. In such situations, individuals should be able to multi-task, reallocating time while foraging to scanning their surroundings, scrounging, monitoring other group members to limit interference from other individuals for access to food, or to maintain spatio-temporal cohesion of the group. In this way, they reduce the high cost that the vigilance posture requires. However, little is known about how much time herbivores invest in apprehensive foraging and vigilance when food density varies, although this issue is crucial for assessment of the costs of awareness in the context of the trade-off between food and safety (Brown 1999).

In African savanna ecosystems, large mammalian herbivores forage in landscapes characterized by high resource heterogeneity (Venter et al. 2003; Gaylard et al. 2003). Large carnivores in these ecosystems are known to influence their prey populations through direct lethal effects (e.g., Sinclair et al. 2003; Grange et al. 2004) and indirect behavioral effects (Valeix et al. 2009a, b). We studied a population of free-ranging impalas (*Aepyceros melampus*), a social antelope experiencing strong predation pressure in a conservation area, the Hwange National Park (Zimbabwe), to investigate how patch attractiveness, group size, and proxies of predation risk affect patterns of individual awareness, decomposed into apprehensive foraging and vigilance. Our study site is on poor soil: Kalahari sands. We designed a fertilization experiment to manipulate the quality of food patches, with enriched plots being characterized by a higher biomass of good quality (green) tissues and nutrients since grasses on more fertile soils have higher nitrogen contents than on poor soils (Prins and Olff 1998). We compared the awareness of individuals foraging on patches of different food quality. The experiment was carried out in the heart of the rainy season so as to minimize the effect of plant senescence on the quality of food patches.

We predicted that, while foraging on enriched plots, individuals should spend less time vigilant, in order to increase acquisition of high quality food (Table 1, Hypothesis 1). Predictions for apprehensive foraging are less intuitive: high quality food may lead to more time spent chewing, head-up (larger bites, reduced search time; Table 1, Hyp. 2.1), but the need to monitor conspecifics may decline (Table 1, Hyp. 2.2). We expected apprehensive foraging to increase with increasing group size, and as the nearest neighbor is closer under a scenario of competition for food (Table 1, Hyp. 3 and 8), but anti-predator vigilance should decrease with increasing group size (Table 1, Hyp. 4). If predation risk was a main driving force, we expected individuals to be more aware, and particularly more vigilant, in areas characterized by lower visibility, i.e. in taller grass (Table 1, Hyp. 5) and closer to cover (Table 1, Hyp. 7), independently of the patch quality (high biomass or nutrients). Finally, since the amount of time needed to handle the grass increases with grass height, we expected apprehensive foraging to increase as well (Table 1, Hyp. 6). If food biomass and predation are both major driving forces, we expected to detect an additive or an interactive effect of these two factors on levels of awareness by the individuals.

Materials and methods

Study area and animals

The fieldwork was conducted in the vicinity of Main Camp in Hwange National Park (HNP) in Zimbabwe (19°00'S, 26°30'E). The study site is an open grassland area of 64 ha surrounded by *Acacia* and *Combretum* bushes, typical of the mixed bushed grassland on nutrient-poor soils of the eastern Kalahari sands (Rogers 1993). Bushes form a natural and visually obstructive boundary of the grassland through which animals move freely. The long-term mean annual rainfall at the site is 606 mm and the rainy season occurs from the end of October to the end of April (Chamaille-Jammes et al. 2007).

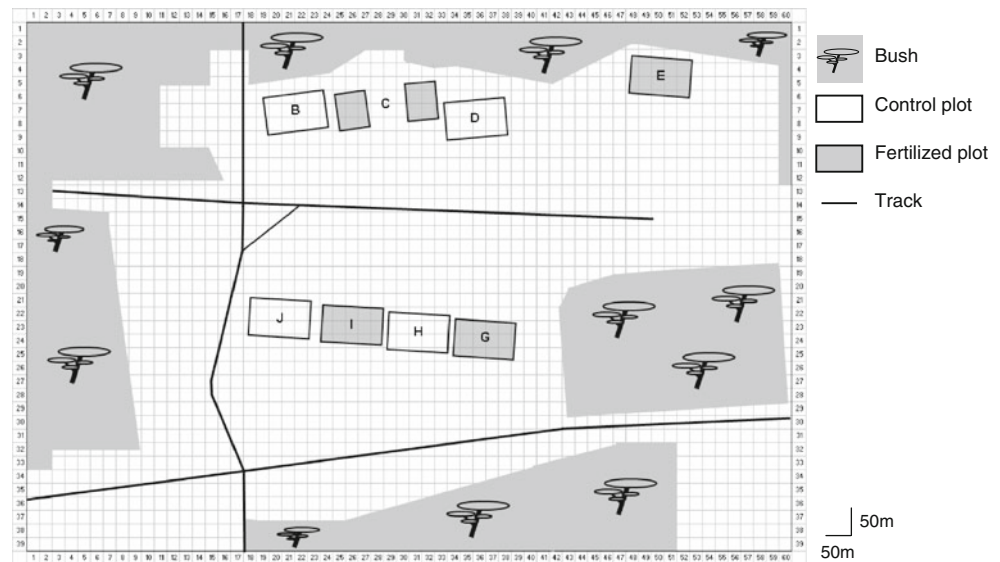
Impala are gregarious and sedentary, and some males are territorial (seasonally or permanently; Estes 1991). Females gather in fairly large groups (Jarman and Jarman 1973). As reproductive behaviors may affect vigilance of all individuals in a group, we conducted our field experiment outside the mating and fawning periods. At the time of the study, January to March 2009 in the wet season, impalas are mostly grazers and foraged mostly in open grasslands. About 50–150 impalas (mainly females and

Table 1 Summary of the predicted relationship between awareness (distinguishing apprehensive foraging and vigilance) and group and environmental factors controlling for date and time of day assuming that time is constraining

Factors	ID hypothesis	Type of time allocation expected to be adjusted	Sign of the relationship	Mechanisms underlying this effect
Patch enrichment (higher biomass and greenness)	1	Vigilance	–	In a rich patch, individuals are expected to increase food acquisition, within acceptable limits of risk taking
	2.1	Apprehensive foraging	–	Re-allocation of time (for detecting predators) while chewing when foraging on patches of high food quality
	2.2		+	Individuals monitor other group members to glean information when food density is low (producer–scrounger theory)
Group size	3	Apprehensive foraging assuming that vigilance is not used for social multi-tasking	+	Social monitoring increases with group size as more group members need to be monitored to limit contest or scramble competition
	4	Vigilance	–	Individual benefits from the presence of other group members (many-eyes effect and dilution risk) to reduce its own vigilance
Grass height	5	Vigilance	+	When visibility decreases, vigilance increases as potential predator are more difficult to detect
	6	Apprehensive foraging	+	As bite size increases when grass is tall, apprehensive foraging increases
Distance to cover	7	Vigilance	–	Since impala anti-predator strategy is mainly based on vigilance and flight, we expect vigilance to increase as distance to cover decreases since bushes are likely to hide ambush predators
Distance to the nearest neighbour	8	Apprehensive foraging	–	When distance to the nearest neighbor decreases, interference competition for food access and scrounging increase

– a decrease of awareness when the considered factor increases, + a positive relationship

Fig. 1 Design of the field experiment manipulating the quality of feeding patches for herbivores in the Main Camp area of Hwange National Park, Zimbabwe



juveniles) foraged each day at the study site during the field session. The impala has sharp vision, is quick to take flight, and is known for its high speed and its spectacular leaps, up to 3 m high and 11 m in length (Estes 1991). Vigilance in impala can therefore be considered to be part of highly developed anti-predator behavior, particularly in open environments.

The main predators of impalas are spotted hyaenas (*Crocuta crocuta*), lions (*Panthera leo*), leopards (*Panthera pardus*), and occasionally cheetahs (*Acinonyx jubatus*) and African wild dogs (*Lycaon pictus*). Young impalas are also preyed upon by black-backed jackals (*Canis mesomelas*). All these predators occur in the study area; lions and hyaenas are common (Valeix et al. 2009a, b).

Experimental design

To investigate how impalas adjust vigilance levels with variation in the quality of their food resources, we designed a field experiment to create enriched patches by manipulating the vegetation using fertilization. The aim was to increase the biomass, and the proportion of the best quality tissues (green, growing ones). Four enriched plots (120 × 60 m) were created at different distances to cover (Fig. 1). We paid particular attention to select plots as homogenous as possible in terms of plant community and grass height. The plots were enriched by a common fertilizer for pastures (N: 3.5%, P₂O₅, 24.4%, S: 11.0% and Zn: 0.5%), at 70 kg/ha. Fertilization was performed in January 2009, 2 weeks before the beginning of the behavioral studies, and was facilitated by rainfall throughout the observations. To measure the effect of fertilization on plant quality (and thus the attractiveness of the patches), we measured grass height and greenness in the enriched and control plots (see Fig. 1)

at the end of February 2009. Using a disk pasture meter, we recorded grass height every 5 m on 60-m transects, giving a total of 44 samples per plot (11 samples × 4 transects). To convert grass height to biomass, we used a calibration equation derived at this site during a previous study, where grass height and biomass were measured by clipping, drying and weighting the green biomass below the disk pasture meter (biomass = 2.5967 × height, adjusted $R^2 = 0.85$, $n = 56$; Chamaille-Jammes, Gignoux, Fritz, unpublished data). Biomass was 14.1% higher in enriched than in control plots ($F_{1-350} = 7.93$, $P = 0.005$). Since herbivores select for green leaf (e.g., Murray and Baird 2008), we tested for an increase in the proportion of green tissues in the enriched plots using photographs of 1 × 1 m quadrats every 10 m on each of the four 60-m transects; the proportion of green tissues were estimated visually (as in Walker 1976; Vanha-Majamaa et al. 2000). The proportion of green tissues was on average 13.1% higher on enriched plots ($F_{1-190} = 19.97$, $P < 0.0001$), and 12.5% higher when controlling for grass height (as the proportion of green tissue decreased with grass height; $F_{1-188} = 26.54$, $P < 0.0001$). We also used these photographs to assess the average grass cover by estimating the proportion of bare soil in each quadrat. The proportion of bare soil was 13.5% lower on enriched plots ($F_{1-190} = 19.97$, $P < 0.0001$). Enriched plots in this experiment therefore have more biomass, a higher proportion of green tissues and less bare ground. The grass biomass available to the impalas on the study area varied between 20 and 150 g/m², and an increase of biomass between these values will lead to an increase in intake in a selective herbivore of this body size (see data for sheep in Spalinger and Hobbs 1992, and gazelles in Wilmshurst et al. 1999).

Behavioral data

We collected behavioral data by videotaping (video camera: Sony DCR-SR30, $\times 20$ optical) focal adult females (to avoid any sex or age effect; e.g., Pays and Jarman 2008), for 5-min periods chosen at random during the daytime. We used recordings only from groups whose predominant activity was foraging, which did not move far during the recording, and whose size and composition did not change during the video sequence. We defined a group on the basis of a maximal separation between adjacent members of 50 m, and on the maintenance of social and spatial cohesion of the group members during the focal sampling (as in Frid 1997, for other mammals). No ambiguities were encountered in defining a group using these criteria; inter-individual distances were very small.

Data were collected from vehicles, respecting a minimal distance of 100 m between the focal group and the observer to minimize disturbance; these impalas were habituated to cars and easy to observe. All female impalas on the study area formed a single clan that was divided into a variable number of groups with marked fusion–fission dynamics (about 30 ear-tagged adult females were individually recognizable). Several individuals were filmed from this group on some days, and the observer took care to avoid filming the same individual twice during the same day. Re-sampling, therefore, represented a negligible part of our dataset.

During the video sampling, the observer recorded the location of the studied females on a field map (Fig. 1) in relation to the enriched plots. The distance to cover was estimated ($D \leq 25$, $25 < D \leq 50$, $50 < D \leq 100$, $100 < D \leq 200$, $D > 200$ m), as it is a commonly used proxy for predation risk (Lima 1990; Burger et al. 2000; Blumstein et al. 2003). The role played by cover (i.e. obstructive or protective) is, however, ambiguous, and depends on many factors such as the time schedules of prey and predators, type of predators (aerial vs. terrestrial, ambush vs. pursuit), and thus expectations on the effect of distance to cover on individual vigilance are not obvious. Visibility around foraging individuals, however, provides a measure of foragers' visual obstruction at a fine scale (Whittingham et al. 2004) and allows clearer expectations. For example, it has been found in socially foraging birds that vigilance increased with a decrease of visibility around prey (Guillemain et al. 2001). Here, we estimated the height of the grass in the patch on which the individuals were foraging. We considered grass to be *short* when it was not above the focal impala's hooves, *medium* when grass height was below the upper part of the metacarpals and *tall*, when grass height reached the tibia. In *tall* grass, the visibility of the focal animal was strongly reduced when feeding in the herb layer. We also recorded the date and time of day, group size and the distance to the

nearest neighbour ($d \leq 2$, $2 < d \leq 5$, $5 < d \leq 10$, $10 < d \leq 20$, $d > 20$ m). The position of the individuals within a group (i.e. peripheral or central; e.g. Blanchard et al. 2008) was impossible to determine during the video sampling because the animals moved constantly when foraging.

To investigate the effect of the variations in grass quality among patches on the behavior of the impalas, it was necessary that animals stayed in the enriched plots during the 5-min video sequences. We sampled 25 impalas foraging inside enriched plots and 65 outside; see Table 2.

An animal was considered to be “aware” when it raised its head above the horizontal, scanning its surroundings, without moving its feet. No ambiguities were encountered in distinguishing an aware from a non-aware animal. We assessed the nature of bouts of awareness distinguishing “apprehensive foraging”, when an animal raised its head while chewing, and “vigilance”, when it raised its head and stopped chewing (see “Introduction”). When an animal engaged in apprehensive foraging and vigilance during the same bout of awareness, we determined the time spent in each activity separately. We extracted the total time spent in awareness, the frequency of awareness, the total time spent in apprehensive foraging, and vigilance from each sequence.

Data analyses

We first investigated whether patch enrichment, distance to cover, grass height, group size, distance to nearest neighbor, and the interactions between these factors affected the total time spent in awareness, the frequency of awareness, and the total time spent in apprehensive foraging and vigilance, controlling for the effects of date, time of day. To achieve normality and homoscedasticity, we log-transformed those four dependent variables. To improve linearity in the relationships between the variables, group size was also log-transformed.

First, we explored factors influencing the total time spent in awareness and the frequency of awareness. Since there was a strong positive correlation between the total time and the frequency (linear mixed-effects model, controlling for the effects of all independent variables cited above and including 2 nested random factors, group identity within plot identity, coefficient \pm SE = 0.548 \pm

Table 2 Sample size and group size of monitored impalas (*Aepyceros melampus*) and type of patches (enriched or not)

Patch type	Individual <i>n</i>	Group size			
		Mean	SE	Min	Max
Not enriched	65	48.0	4.32	2	108
Enriched	25	47.6	7.06	5	93

0.053, $F_{1-24} = 147.675$, $P < 0.0001$, pseudo $R^2 = 0.79$), we used the frequency of awareness only. We computed a linear mixed-effect model including the independent variables patch enrichment, grass height, distance to cover, distance to the nearest neighbor, Log-transformed (group size), time of day, date and their interactions, and including two nested random factors, group identity within plot identity. To reduce the large number of degrees of freedom in our statistical procedures triggered by the large number of continuous and categorical variables, we included only two-way interactions which were interpretable in terms of mechanisms influencing frequency of awareness (see Table 3).

Some individuals exhibited only apprehensive foraging (and not vigilance, the costly posture) whereas other exhibited both apprehensive foraging and vigilance, and we therefore investigated which factors affected the probability of exhibiting the costly posture of vigilance (0: no vigilance and 1: presence of vigilance in the 5-min video sequence). We ran a generalised linear mixed-effects model with the Laplace procedure (binomial, link: Logit) including the same independent variables and random factors listed in the previous procedure.

Finally, for the impalas exhibiting the two forms of awareness in their 5-min sequences, the log-transformed time spent in vigilance was not significantly correlated with the log-transformed time spent in apprehensive foraging (linear mixed-effects model, $F_{1-24} = 2.914$, $P = 0.110$). We therefore investigated separately the factors influencing these two response variables of time allocation. We computed linear mixed-effect models including all independent variables and their interactions as fixed factors listed above,

including two nested random factors, group identity within plot identity.

The statistical analyses were performed using R 2.10.1 (R Development Core Team 2010).

Results

On average (\pm SE), the impalas were aware (either apprehensive foraging or vigilance) for 43 s (± 3.6) of the 5-min sequences, which represented 14% of their time. The number of awareness acts per min was 1.8 (± 0.01); and most of their awareness time was apprehensive foraging ($81\% \pm 0.01$). We present first the results for awareness, then for the frequency of vigilance, and finally for time spent in apprehensiveness and vigilance.

Factors influencing the frequency of awareness

Patch enrichment and grass height significantly affected the frequency of awareness (i.e. number of head-ups/min, highly correlated with time spent in awareness) (Table 3). The impalas were aware less often when the grass was short, and the model suggested that this was also true when foraging on enriched patches. Visual inspection of the data suggested that this may be true only when grass was short, although the enrichment—grass height interaction was not found to be significant (Fig. 2; Table 3).

Controlling for the effects of date and time of day, we did not detect any effect of group size, distance to cover and distance to the nearest neighbor or of the two-way interactions (Table 3).

Table 3 Factors influencing the log-transformed frequency of awareness of female impalas (the sum of apprehensiveness + vigilance)

Factors	No. <i>df</i>	Den. <i>df</i>	<i>F</i>	<i>P</i>	Coeff \pm SE
Intercept	1	47	41.920	<0.0001	0.030 \pm 0.010
Patch enrichment	1	13	5.601	0.034	Yes: -0.049 ± 0.024
Grass height	2	13	5.649	0.017	Medium: 0.218 ± 0.084 ($P = 0.015$) Tall: 0.255 ± 0.069 ($P = 0.001$)
Log group size	1	47	0.001	0.970	
Distance to cover	4	13	0.843	0.522	
Distance to the nearest neighbor	3	13	1.594	0.239	
Date	1	47	0.519	0.475	
Time	1	13	0.145	0.710	
Log group size \times patch enrichment	1	13	1.280	0.278	
Grass height \times patch enrichment	2	13	1.398	0.282	
Log group size \times grass height	2	13	0.179	0.838	
Log group size \times distance to cover	4	13	0.427	0.787	

Two nested random factors, group identity within plot identity, were included and contributed to estimate error term (intercept). Log (Group size), date and time of day were considered as continuous. Enriched patch (Yes, *Control = No*), grass height (*short*, medium, tall), distance to cover ($D \leq 25$, $25 < D \leq 50$, $50 < D \leq 100$, $100 < D \leq 200$, $D > 200$ m) and distance to the nearest neighbor ($d \leq 2$, $2 < d \leq 5$, $5 < d \leq 10$, $10 < d \leq 20$, $d > 20$ m) were categorical (the classes used as references are italicised in the legends)

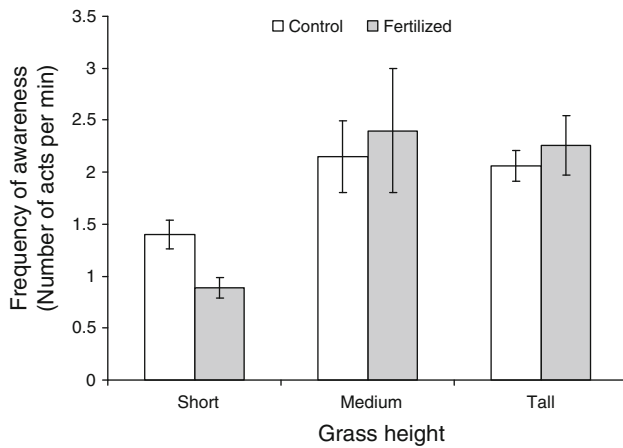


Fig. 2 Controlling for group size of impalas (*Aepyceros melampus*), effect of patch enrichment and grass height on the frequency of awareness in the wet season 2009 in Hwange National Park, Zimbabwe. See Table 2 for statistics

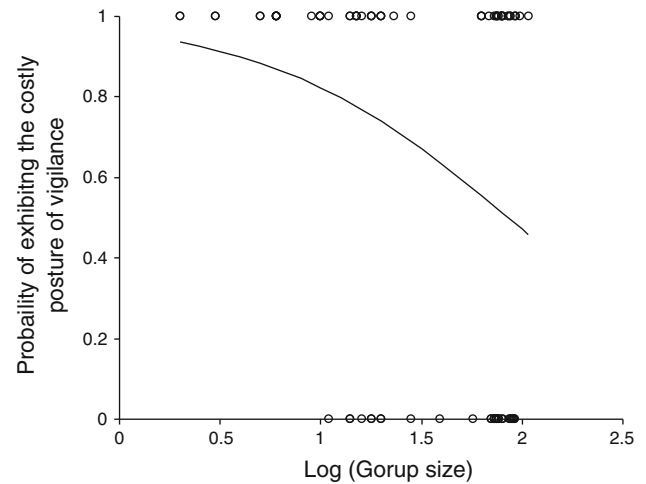


Fig. 3 Effect of log-transformed group size on the probability of exhibiting vigilance in the wet season 2009 in Hwange National Park, Zimbabwe

Probability of vigilance

Over the 90 foraging female impalas studied, 31 exhibited apprehensive foraging only (and not vigilance, the costly posture) whereas 49 exhibited both apprehensive foraging and vigilance. The probability of exhibiting a vigilance posture during the 5-min monitoring period decreased with group size (Table 4; Fig. 3). However, we did not detect any significant effect of distance to cover, patch enrichment, distance to the nearest neighbor, or of the two-way interactions.

Factors affecting time spent in apprehensive foraging and vigilance

Forty-nine individuals exhibited the two forms of awareness, with on average (\pm SE) 12.2 ± 2.4 s in vigilance and

30.6 ± 2.3 s in apprehensive foraging in the 5-min video sequences.

Grass height significantly affected time spent in apprehensive foraging with individuals spending more time in apprehensive foraging when the grass was tall (Table 5); the other variables, in particular enrichment, had no significant effects. The interaction between grass height and plot enrichment significantly affected the time spent in vigilance (Table 5). According to the coefficients derived for that interaction when the control patches and short grass are used as references (Table 5), Fig. 4 illustrates that impalas foraging on short and medium-height grass spent less time vigilant on enriched patches compared to control ones, and the pattern inverted when the grass was tall.

Table 4 Factors influencing the probability for female impalas to exhibit a vigilance posture during the 5-min monitoring period

Factors	χ^2	df	P	Coeff \pm SE
Patch enrichment	0.207	1	0.649	
Grass height	1.090	2	0.580	
Log group size	12.404	1	0.0004	-1.650 ± 0.580
Distance to cover	9.135	4	0.060	
Distance to the nearest neighbor	3.972	3	0.265	
Date	0.001	1	0.999	
Time	0.308	1	0.579	
Log group size \times patch enrichment	1.166	1	0.280	
Grass height \times patch enrichment	0.947	2	0.623	
Log group size \times grass height	0.666	2	0.717	

Two nested random factors, group identity within plot identity, were included and contributed to estimate error term (intercept). Log (Group size), date and time of day were considered as continuous. Enriched patch (Yes, *Control = No*), grass height (*short*, medium, tall), distance to cover ($D \leq 25$, $25 < D \leq 50$, $50 < D \leq 100$, $100 < D \leq 200$, $D > 200$ m) and distance to the nearest neighbor ($d \leq 2$, $2 < d \leq 5$, $5 < d \leq 10$, $10 < d \leq 20$, $d > 20$ m) were categorical (classes used as references are italicised in the legends)

Table 5 Factors influencing the time spent in (A) vigilance, log-transformed, and (B) apprehensive foraging in female impalas exhibiting the two forms of time allocation in their 5-min sequences

Factors	No. <i>df</i>	Den. <i>df</i>	<i>F</i>	<i>P</i>	Coeff ± SE
(A) Log-transformed time spent in vigilance (pseudo $R^2 = 0.54$)					
Intercept	1	20	203.7246	<0.0001	1.022 ± 0.170
Patch enrichment	1	20	2.995	0.092	
Grass height	2	20	1.398	0.270	
Log group size	1	20	3.645	0.071	
Distance to cover	4	20	1.849	0.159	
Distance to the nearest neighbor	3	20	1.761	0.187	
Log group size × patch enrichment	1	20	0.972	0.336	
Grass height × patch enrichment	2	20	6.075	0.009	Medium on fertilized: 0.149 ± 0.589 ($P = 0.802$) Tall on fertilized: 1.381 ± 0.397 ($P = 0.002$)
Log group size × grass height	2	20	0.121	0.887	
(B) Log-transformed time spent in apprehensive foraging (pseudo $R^2 = 0.35$)					
Intercept	1	20	1,534.835	<0.0001	1.238 ± 0.069
Patch enrichment	1	20	2.162	0.157	
Grass height	2	20	5.485	0.013	Medium: 0.147 ± 0.103 ($P = 0.163$) Tall: 0.238 ± 0.084 ($P = 0.015$)
Log group size	1	20	0.0002	0.910	
Distance to cover	4	20	0.596	0.670	
Distance to the nearest neighbor	3	20	1.121	0.364	
Log group size × patch enrichment	1	20	0.241	0.629	
Grass height × patch enrichment	2	20	1.901	0.176	
Log group size × grass height	2	20	0.879	0.431	

Two nested random factors, group identity within plot identity, were included and contributed to estimate error term (intercept). Log (Group size) was considered as continuous. Enriched patch (Yes, *Control = No*), grass height (*short*, medium, tall), distance to cover ($D \leq 25$, $25 < D \leq 50$, $50 < D \leq 100$, $100 < D \leq 200$, $D > 200$ m) and distance to the nearest neighbor ($d \leq 2$, $2 < d \leq 5$, $5 < d \leq 10$, $10 < d \leq 20$, $d > 20$ m) were categorical (classes used as references are italicised in the legends)

Discussion

This fertilization experiment allowed us to investigate the factors driving individual awareness, distinguishing between apprehensive foraging (i.e. when the individual is monitoring its surroundings while chewing) and vigilance (characterized by a marked posture of alertness leading to the disruption of the ingestion process), under conditions where the availability of food resources, proxies of the risk of predation and group size, varied.

Both patch enrichment and grass height significantly affected several aspects of the anti-predator behavior of impalas (awareness, apprehensive foraging, and vigilance) either independently or in interaction. Impalas spent less time in awareness when foraging on enriched plots, which were characterized by a higher food biomass and quality. Our detailed results on apprehensive foraging and vigilance suggest that this was essentially due to an adjustment of the time spent in vigilance in short and medium grass and not the time devoted to apprehensive foraging. The hypothesis that individuals foraging on poor quality patches should be more vigilant than if they are foraging on high quality

patches is therefore supported (Table 1, Hyp. 1), as is the hypothesis of re-allocation of time for predator detection (Table 1, Hyp 2.1). A negative correlation between the time allocated to managing predation risk and abundance of food resources has been predicted by theory (Brown 1999) and already reported in birds (Fritz et al. 2002; Butler et al. 2005) and mammals, including herbivores (LaGory 1986) and carnivores (Pangle and Holekamp 2010). In Hwange National Park, and particularly in our study area, enriched patches are rare in the landscape. It is therefore probable that the observed decrease of individual vigilance with patch attractiveness is due to impalas increasing their rate of food intake on the rich patches to maximise acquisition of high-quality resources. That tactic might also be reinforced when impalas forage in large groups (as in this study) since group members can monopolize only a small part of these patches. The opposite pattern, i.e. a positive relationship between vigilance and food density, has been reported in some birds (Johnson et al. 2001; Randler 2005; Amano et al. 2006) and mammals (Fortin et al. 2004; Benhaïem et al. 2008). Thus, the variability of the trend between vigilance and food density

across species is context dependent. Indeed, the interplay between abundance (or rarity) of richer patches in the landscape, predation pressure, intra-group competition and individual energetic requirements should promote different behavioral tactics.

Our findings do not support the hypothesis that individuals foraging on poorer patches dedicate more time to apprehensive foraging to monitor other group members to glean information on richer patches (Table 1, Hyp. 2.2). This prediction was based on the principle that social vigilance (i.e. the time that individuals spent scanning other group members) should increase as scrounging opportunities become more available (Beauchamp 2008; see Giraldeau and Beauchamp 1999 for conditions that promote scrounging opportunities). Alternatively, one could have expected less apprehensive foraging on poorer patches since scrounging would be a less valuable activity since fewer food patches are discovered by producers. In the event, no significant relationship was found between patch richness and apprehensive foraging at all. Further investigations of the structure of the foraging bout and of key parameters, for instance chewing duration, will be required to disentangle these hypotheses.

Grass height, and thus the perceived predation risk, significantly affected the frequency of awareness, the time spent in apprehensive foraging, and the time spent in vigilance, with impalas being more alert and vigilant in taller grass. These results support the hypotheses that apprehensive foraging increases as grass height, and therefore bite size, increases (Table 1, Hyp. 6) and vigilance increases when potential predators are more difficult to detect (Table 1, Hyp. 5). This latter pattern has been found in socially foraging birds in which vigilance increased with a decrease of visibility around prey (Guillemain et al. 2001). The increase of vigilance with grass height strongly suggests a need to improve the perception of predation risk when an animal's vision is obstructed locally.

Distance to cover (a proxy of perception of predation risk at a larger scale) did not affect the vigilance of the impalas foraging in the study area (Table 1, Hyp. 7 not supported). While similar results have been reported in prey species (Blumstein et al. 2003), other studies have reported that vigilance of prey may either increase (Carrascal and Alonso 2006; Pays et al. 2009) or decrease (Burger et al. 2000; 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 (Lima 1990). As described in “Materials and methods”, impalas have to deal with a large range of potential predators both ambush and pursuit. It is therefore not surprising that distance to cover is not a useful proxy for predation risk in the context of Hwange.

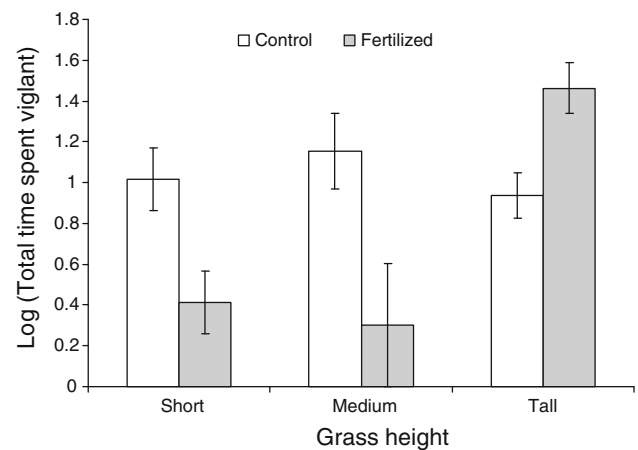


Fig. 4 Effect of the interaction between patch enrichment and grass height on the log-transformed total time spent in vigilance in the wet season 2009 in Hwange National Park, Zimbabwe

Interestingly, the interaction between fertilization and grass height significantly influenced the time spent in vigilance. The pattern revealed (Fig. 4) suggests that food patch quality may be the driving factor influencing vigilance when visibility is high (low perceived predation risk) in contrast to situations when visibility is low (tall grass), where the risk of predation is the main driver, and herbivores may need to invest in vigilance, whatever the characteristics of the food patches.

The probability of exhibiting a vigilant posture (i.e. a costly but high quality posture for predator detection) decreased when group size increased, whether impalas were foraging on control or enriched areas. This result supports classic predictions (Table 1, Hyp. 4) reflecting the increased safety of prey animals in larger groups (Lima 1995). 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 group size; Hamilton 1971), and a many-eyes effect (i.e. the chance that at least one individual in a group is vigilant at any given moment increases with group size; Pulliam 1973), individuals can afford to decrease their own level of vigilance in larger groups. This pattern has been reported in many taxa (Roberts 1996; Childress and Lung 2003; 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 groups may allow animals to rely on apprehensive foraging, whereas animals in smaller groups have sometimes to dedicate a large amount of their time to vigilance since the group size is too small to rely on the many-eyes effect.

The functional implications of the differential strength of the group-size effect on vigilance, between groups according to the richness of their patch, has already been

addressed with regard to both the natural tendency that foragers form larger groups in areas of higher food density (Clark and Mangel 1984, 1986; Lima 1990), and the existence of a time constraint on foraging (McNamara and Houston 1992; Krause and Ruxton 2002; Beauchamp 2009). There is likely to be more competition for food in large groups and consequently interference between individuals, and the associated social vigilance are expected to increase with group size (Sansom et al. 2008; Kaspersson et al. 2010; Favreau et al. 2010). The lack of any positive effect of group size on apprehensive foraging, and of any effect of distance to the nearest neighbor in our experiment, does not support social monitoring and scrambling competition hypotheses (Table 1, Hyp. 3 and 8). This lack of any effect might be explained by the size of our enriched plots. Many fish (Robb and Grant 1998), birds (Goldberg et al. 2001; Johnson et al. 2004) and mammals (Monaghan and Metcalfe 1985) become non-aggressive when food patches are large (see resource defence theory; Myers et al. 1981). Indeed, Grant (1993) showed more generally that patch size can influence the decisions of individual foragers whether or not to use aggression during social foraging, which would in turn lead to an increase in social vigilance with group size.

The results, overall, support classical predictions regarding the effects of food resources, visibility, and group size on vigilance behavior. No single regulating mechanism determined the behavior of the animals. This study, using an original in situ experimental manipulation of food resources, provides a clear illustration of the trade-off faced by herbivores between food and safety. Indeed, patch enrichment and grass height played a key role in prey awareness and particularly vigilance, and their interactive effect has been brought to light. Our study provides less evidence of the strong involvement of processes based on producer–scrounger hypotheses to determine the level of time allocation in this species, since apprehensive foraging was not influenced by group size or distance to the nearest neighbor in our context. However, more work, particularly experimental, is needed to improve our knowledge on the link between forms of awareness (apprehensive foraging, vigilance) and their functions (predator detection, social monitoring).

Acknowledgments The Director General of the Zimbabwe Parks and Wildlife Management Authority is acknowledged for providing the opportunity to carry out this research. We are particularly grateful to Dr. H. Madzikanda for his long term support and friendship. Our warm thanks also go to Mr. A. Musakwa, the Area Manager, for his support and understanding, as well as to the Parks Senior ecologist G. Mtare. This study was done in the framework of the HERD program (Hwange Environmental Research Development), funded by the CNRS INEE (“Institut Ecologie et Environnement”, “Zones Ateliers” programme, the Agence National de la Recherche FEAR project (ANR-08-BLAN-0022), the CIRAD and the French

“Ministère des Affaires Etrangères”, and the “Ambassade de France au Zimbabwe”. We are grateful to B.P. Kotler and an anonymous referee for their valuable comments on a previous version of the manuscript. We would also like to thank the whole HERD team for allowing it to happen. Finally, we want to acknowledge here the memory of our friend, Bertrand Eliotout.

Conflict of interest Experiments comply with the current laws of the country in which the experiments were performed. The authors declare that they have no conflict of interest.

References

- Ale SB, Brown JS (2007) The contingencies of group size and vigilance. *Evol Ecol Res* 9:1263–1276
- Amano T, Ushiyama K, Fujita G, Higuchi H (2006) Costs and benefits of flocking in foraging white-fronted geese (*Anser albifrons*): effects of resource depletion. *J Zool* 269:111–115
- Baker JD, Stillman RA, Smart SL, Bullock JM, Norris KJ (2011) Are the costs of routine vigilance avoided by granivorous foragers? *Funct Ecol* (in press)
- Barnard CJ, Sibly RM (1981) Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Anim Behav* 29:543–550
- Beauchamp G (2008) A spatial model of producing and scrounging. *Anim Behav* 76:1935–1942
- Beauchamp G (2009) How does food density influence vigilance in birds and mammals? *Anim Behav* 78:223–231
- Beauchamp G (2010) Relationship between distance to cover, vigilance and group size in staging flocks of semipalmated sandpipers. *Ethology* 116:645–652
- Benhaiem S, Delon M, Lourtet B, Cargnelutti B, Aulagnier S, Hewison AJM, Morellet N, Verheyden H (2008) Hunting increases vigilance levels in roe deer and modifies feeding site selection. *Anim Behav* 76:611–618
- Blanchard P, Fritz H (2007) Induced or routine vigilance while foraging. *Oikos* 116:1603–1608
- Blanchard P, Sabatier R, Fritz H (2008) Within-group spatial position and vigilance: a role also for competition? The case of impalas with a controlled food supply. *Behav Ecol Sociobiol* 62:1863–1868
- Blumstein DT, Daniel JC, Sims RA (2003) Group size but not distance to cover influences agile wallaby (*Macropus agilis*) time allocation. *J Mammal* 84:197–204
- Brown JS (1999) Vigilance, patch use, and habitat selection: foraging under predation risk. *Evol Ecol Res* 1:49–71
- 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
- Butler SJ, Whittingham MJ, Quinn JL, Cresswell W (2005) Quantifying the interaction between food density and habitat structure in determining patch selection. *Anim Behav* 69:337–343
- Carrascal LM, Alonso CL (2006) Habitat use under latent predation risk. A case study with wintering forest birds. *Oikos* 112:51–62
- Chamaillé-Jammes S, Fritz H, Murindagomo F (2007) Detecting climate changes of concerns in highly variable environment: quantiles regressions reveal that droughts worsen in Hwange National Park, Zimbabwe. *J Arid Environ* 71:321–326
- Childress MJ, Lung MA (2003) Predation risk, gender and the group effect: does elk vigilance depend upon the behaviour of conspecifics? *Anim Behav* 66:389–398
- Clark CW, Mangel M (1984) Foraging and flocking strategies—Information in an uncertain environment. *Am Nat* 123:626–641

- Clark CW, Mangel M (1986) The evolutionary advantages of group foraging. *Theor Pop Biol* 30:45–75
- Dall SRX, Kotler BP, Bouskila A (2001) Attention, apprehension and gerbils searching in patches. *Ann Zool Fenn* 38:15–23
- Estes RD (1991) The behavior guide to African mammals. University of California Press, Berkeley
- Favreau FR, Goldizen AW, Pays O (2010) Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. *Proc R Soc Lond B* 277:2089–2095
- Fernández-Juricic E, Beauchamp G, Bastain E (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
- Fritz H, Guillemain M, Durant D (2002) The cost of vigilance for intake rate in the mallard (*Anas platyrhynchos*): an approach through foraging experiments. *Ethol Ecol Evol* 14:91–97
- Gaylard A, Owen-Smith N, Redfern J (2003) Surface water availability: implications for heterogeneity and ecosystem processes. In: du Toit JT, Rogers KH, Biggs HC (eds) *The Kruger experience. Ecology and management of savanna heterogeneity*. Island Press, Washington, pp 171–188
- Giraldeau LA, Beauchamp G (1999) Food exploitation: searching for the optimal joining policy. *Trends Ecol Evol* 14:102–106
- Goldberg JL, Grant JWA, Lefebvre L (2001) Effects of the temporal predictability and spatial clumping of food on the intensity of competitive aggression in the Zenaida dove. *Behav Ecol* 12:490–495
- Grange S, Duncan P, Gaillard JM, Sinclair ARE, Gogan PJP, Packer C, Hofer H, East M (2004) What limits the Serengeti zebra population? *Oecologia* 140:523–532
- Grant JWA (1993) Whether or not to defend? The influence of resource distribution. *Mar Behav Physiol* 23:137–153
- Guillemain M, Duncan P, Fritz H (2001) Switching to a feeding method that obstructs vision increases head-up vigilance in dabbling ducks. *J Avian Biol* 32:345–350
- Hamilton WD (1971) Geometry for the selfish herd. *J Theor Biol* 31:295–311
- Hochman V, Kotler BP (2007) Patch use, apprehension, and vigilance behavior of Nubian Ibex under perceived risk of predation. *Behav Ecol* 18:368–374
- Illius AW, FitzGibbon C (1994) Costs of vigilance in foraging ungulates. *Anim Behav* 47:481–484
- Jarman MV, Jarman PJ (1973) Daily activity of impala. *East Afr Wildl J* 11:75–92
- Johnson CA, Giraldeau LA, Grant JW (2001) The effect of handling time on interference among house sparrows foraging at different seed densities. *Behaviour* 138:597–614
- Johnson CA, Grant JWA, Giraldeau LA (2004) The effect of patch size and competitor number on aggression among foraging house sparrows. *Behav Ecol* 15:412–418
- Kaspersson R, Hojesjo J, Pedersen S (2010) Effects of density on foraging success and aggression in age-structured groups of brown trout. *Anim Behav* 79:709–715
- Kotler BP, Brown JS, Dall SRX, Gresser S, Ganey D, Bouskila A (2002) Foraging games between owls and gerbils: temporal dynamics of resource depletion and apprehension in gerbils. *Evol Ecol Res* 4:495–518
- Kotler BP, Brown JS, Bouskila A (2004) Apprehension and time allocation in gerbils: the effects of predatory risk and energetic state. *Ecology* 85:917–922
- Kotler BP, Brown JS, Mukherjee S, Berger-Tal O, Bouskila A (2010) Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance, and state dependent foraging. *Proc R Soc Lond B* 277:1469–1474
- Krause J, Ruxton GD (2002) *Living in groups*. Oxford University Press, Oxford
- LaGory KE (1986) Habitat, group size, and the behaviour of white-tailed deer. *Behaviour* 98:168–179
- Lazarus J (1979) The early warning function of flocking in birds: an experimental study with captive quail. *Anim Behav* 27:855–865
- Lima SL (1990) Protective cover and the use of space: different strategies in finches. *Oikos* 58:151–158
- Lima SL (1995) Back to the basics of antipredatory vigilance: the group size effect. *Anim Behav* 49:11–20
- Lung MA, Childress MJ (2006) The influence of conspecifics and predation risk on the vigilance of elk (*Cervus elaphus*) in Yellowstone National Park. *Behav Ecol* 18:12–20
- Makowska IJ, Kramer DL (2007) Vigilance during food handling in grey squirrels, *Sciurus carolinensis*. *Anim Behav* 74:153–158
- McNamara JM, Houston AI (1986) The common currency for behavioural decisions. *Am Nat* 127:358–378
- McNamara JM, Houston AI (1992) Evolutionarily stable levels of vigilance as a function of group size. *Anim Behav* 43:641–658
- Monaghan P, Metcalfe NB (1985) Group foraging in wild brown hares: effects of resource distribution and social status. *Anim Behav* 33:993–999
- Murray RG, Baird DR (2008) Resource-ratio theory applied to large herbivores. *Ecology* 89:1445–1456
- Myers JP, Connors PG, Pitelka FA (1981) Optimal territory size and the sanderling: compromises in a variable environment. In: Kamil AC, Sargent TD (eds) *Foraging behavior: ecological, ethological and psychological approaches*. Garland Press, New York, pp 135–158
- Pangle WM, Holekamp KE (2010) Functions of vigilance behaviour in a social carnivore, the spotted hyaena, *Crocuta crocuta*. *Anim Behav* 80:257–267
- Pays O, Jarman PJ (2008) Does sex affect individual and collective vigilance in the eastern grey kangaroo? *Behav Ecol Sociobiol* 62:757–767
- Pays O, Renaud PC, Loisel P, Petit M, Gerard JF, Jarman PJ (2007) Prey synchronize their vigilant behaviour with other group members. *Proc R Soc Lond B* 274:1287–1291
- Pays O, Dubot AL, Jarman PJ, Loisel P, Goldizen AW (2009) Vigilance and its complex synchrony in the red-necked pademelon, *Thylogale thetis*. *Behav Ecol* 20:22–29
- Popp JW (1988) Effects of food-handling time on scanning rates among American goldfinches. *Auk* 105:384–385
- Prins HHT, Olf H (1998) Species richness of African grazer assemblages: towards a functional explanation. In: Newbury DM, Prins HHT, Brown ND (eds) *Dynamics of tropical communities*. Blackwell, Oxford, pp 449–490
- Pulliam HR (1973) On the advantages of flocking. *J Theor Biol* 38:419–422
- R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Randler C (2005) Coots *Fulica atra* reduce their vigilance under increased competition. *Behav Proc* 68:173–178
- Raveh A, Kotler BP, Abramsky Z, Krasnov BR (2011) Driven to distraction: detecting the hidden costs of flea parasitism through foraging behaviour in gerbils. *Ecol Lett* 14:47–51
- Robb SE, Grant JWA (1998) Interactions between the spatial and temporal clumping of food affect the intensity of aggression in Japanese medaka. *Anim Behav* 56:29–34
- Roberts G (1996) Why individual vigilance declines as group size increases. *Anim Behav* 51:1077–1086

- Rogers CML (1993) A woody vegetation survey of Hwange national park. Department of National Parks and Wildlife Management, Harare
- Roth TC, Lima SL, Vetter WE (2006) Determinants of predation risk in small wintering birds: the hawk's perspective. *Behav Ecol Sociobiol* 60:195–204
- Sansom A, Cresswell W, Minderman J, Lind J (2008) Vigilance benefits and competition costs in groups: do individual redshanks gain an overall foraging benefit? *Anim Behav* 75:1869–1875
- Sinclair ARE, Mduma S, Brashares JS (2003) Patterns of predation in a diverse predator-prey system. *Nature* 425:288–290
- Sirof E, Pays O (2011) On the dynamics of predation risk perception for a vigilant forager. *J Theor Biol* 276:1–7
- Spalinger DE, Hobbs NT (1992) Mechanisms of foraging in mammalian herbivores: new models of functional response. *Am Nat* 140:325–348
- Valeix M, Loveridge AJ, Chamaillé-Jammes S, Davidson Z, Murindagomo F, Fritz H, Macdonald DW (2009a) Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology* 90:23–30
- Valeix M, Fritz H, Loveridge AJ, Davidson Z, Hunt JE, Murindagomo F, Macdonald DW (2009b) Does the risk of encountering lions influence African herbivore behaviour at waterholes? *Behav Ecol Sociobiol* 63:1483–1494
- Vanha-Majamaa I, Salemaa M, Tuominen S, Mikkola K (2000) Digitized photographs in vegetation analysis—a comparison of cover estimates. *Appl Veg Sci* 3:89–94
- Venter FJ, Scholes RJ, Eckhardt HC (2003) The abiotic template and its associated vegetation pattern. In: du Toit JT, Rogers KH, Biggs HC (eds) *The Kruger experience. Ecology and management of savanna heterogeneity*. Island Press, Washington, pp 83–129
- Walker BH (1976) An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. *S Afr J Wildl Res* 6:1–32
- Whittingham MJ, Butler SJ, Quinn JL, Cresswell W (2004) The effect of limited visibility on vigilance behaviour and speed of predator detection: implications for the conservation of granivorous passerines. *Oikos* 106:377–385
- Wilmschurst JF, Fryxell JM, Colucci PE (1999) What constrains daily intake in Thomson's gazelles? *Ecology* 80:2338–2347