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Between-gender differences in vigilance do not necessarily lead to differences in foraging-vigilance tradeoffs

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Abstract When prey are time limited in their access to food, any trade-off involving time should ultimately affect their intake rate. In many herbivores, males and females experience different ecological pressures affecting their survival and reproduction because of differences in morphology, physiology and energy/nutrient requirements. If males and females have different vigilance strategies that affect their intake rates differently, they will suffer different foraging costs. This is particularly relevant in sexually monomorphic herbivores, where the two sexes have similar basal energy/nutrient requirements and risk of predation. We investigated how gender, reproductive status, age, group size, predation risk, and food biomass affected vigilance, intake rate, and their trade-off in a monomorphic species,

the plains zebra (*Equus quagga*). Males were more vigilant than females, and lactating females were less vigilant than other females; the levels of vigilance were low (ca. 10 % of feeding time). The effects on time spent feeding, bite rates and intake rates were small and statistically not significant. Reproductive status did not affect the strength of the relationship between vigilance and intake rate, but intake rates increased with group size and, for adult females, were higher in tall grass. While gender and reproductive status were major drivers of vigilance, and group size and food biomass of the rate of food intake, males and females adjust their bite rates and food intake with vigilance in similar ways. Our results support the hypothesis that in monomorphic animals, males and females seem to make similar trade-offs (i.e. adjustments) between vigilance and intake rate.

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Our work complied with the current laws of Zimbabwe. It was conducted under permits from the Director General of the Zimbabwe Parks and approved by the Wildlife Management Authority [reference D/M/Gen/(T), permit 23(1)(c)(ii) 01/2010]. The long-term individual-based study on zebra population dynamics started in 2004 is supervised by Dr P. Duncan and is part of the programme of the CNRS ZA/LTER Hwange directed by Dr H. Fritz under permits from the authorities cited above.

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Introduction

Animals commonly trade-off time among feeding, avoiding predators and acquiring information on competitors (Brown et al. 1999; Beauchamp 2009; Krause and Ruxton

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2002). Vigilance thus creates opportunity costs, since the time spent detecting predators or monitoring conspecifics is expected to reduce the time available for feeding. Adjustments of vigilance are particularly important when prey have strong time constraints on foraging (e.g. Ale and Brown 2007 or Beauchamp 2009 for a review). In particular, the McNamara and Houston model (1992) shows that when animals are limited by time in their access to food, any trade-off involving time ultimately affects their food intake rate. While the constraints on vigilance activity (including the presence of competitors, high predation risk or poor-quality food resources) have been well studied (Sansom et al. 2008; Pays et al. 2012; Périquet et al. 2012) in group-forming prey species, the occurrence and importance of differences between the sexes in adjustments of intake rate with vigilance are less well understood.

Understanding how food intake rates are affected by vigilance requires identifying the constraints acting on this trade-off. One promising way to study this trade-off is to investigate the strength of the relationship between the time spent in vigilance and food intake (Cowlshaw et al. 2004). It has been reported that food intake decreases when vigilance increases both in mammals and birds (Fortin et al. 2004; Baker et al. 2011): studying this issue is relatively easy in granivores since bite sizes are rather constant. In grazers, however, calculating intake rates is difficult: bite rates are easy to count, but intake is maximal at intermediate bite rates, since bite size (a major determinant of intake rates) varies strongly with grass height (Spalinger and Hobbs 1992). Bite size cannot be measured accurately in the field, so in this study of zebras we use knowledge from work on another equid of similar size (see “Materials and methods” section) to estimate intake rates.

The question of whether males and females make different trade-offs between vigilance and intake rate (i.e. exhibit significant differences in the strength of this relationship) is difficult to investigate, since mechanisms underlying any between-gender differences could come from differences in vigilance, in intake rate or both. For example, Pays and Jarman (2008) reported several mechanisms explaining differences in vigilance between males and females and predicted different patterns for the sexes. There are two main hypotheses on vigilance relevant for gregarious species. The first suggests that direct interference between males (e.g. for territoriality or for access to females) requires them to monitor the presence and activity of potential rivals carefully (Baldellou and Henzi 1992) particularly if an oestrous female is present. Secondly, in herbivores, females are particularly constrained in their time allocation, as their nutrient requirements and food intake may increase strongly during lactation [by a factor >2 (Speakman 2008); for sheep see Penning et al. (1995); for feral horses see

Rubenstein (1986)]. Moreover, between-gender differences in diet selectivity can also trigger differences in feeding activity (Clutton-Brock et al. 1982). Because of these differences between the sexes in absolute energy requirements and in inter-individual interference, males and females may have functional reasons for differing in their vigilance and intake rates, especially if their reproductive status requires them to invest differently in social monitoring, predator detection or food acquisition. Predicting the strength of the difference between the two sexes in their vigilance-food trade-off therefore requires that reproductive status, age, predation risk, social context and food availability are controlled for.

In African savannah ecosystems, large mammalian herbivores forage in landscapes with high resource heterogeneity (Gaylard et al. 2003; Venter et al. 2003). Responses of prey to heterogeneity in their food resources are strongly affected by large carnivores, principally through indirect behavioural effects (Valeix et al. 2009; Thaker et al. 2010), but little is known about differences between the sexes in these trade-offs. We studied a population of wild plains zebras (*Equus quagga*) in Hwange National Park (HNP), Zimbabwe. As zebras are not sexually dimorphic in their body size, males and females have similar basal energy/nutrient requirements. Indeed, previous studies have shown that the time budgets of male and female zebras are similar, and their activities are highly synchronised. Further, reproductive state matters, as lactating females have higher bite rates than either non-lactating females or males (Neuhaus and Ruckstuhl 2002). Zebras are extremely social (Rubenstein and Hack 2004) and are one of the preferred prey of lions (Hayward and Kerley 2005). In HNP, they experience heavy predation (Grange et al. 2015), as in other ecosystems (Grange and Duncan 2006; Rubenstein 2010) and are likely to spend at least 14–16 h day⁻¹ feeding. Indeed, equids have a high intake feeding strategy (Duncan et al. 1990) which leads them to spend over 50 % of 1 day feeding; about 25 % of their time is spent resting, so a maximum of 25 % remains for all the other activities including vigilance, unless they multitask (sensu Fortin et al. 2004). For instance, female plains zebras feed for 69 % of their time in the dry season in Kenya, and 57 % in the wet season (Gakahu 1982). By comparison, other medium-sized herbivores are less constrained, as they almost always spend less than 50 % of the time feeding (Owen-Smith 1988; Fig. 6.4 for data on zebras and several other species).

We investigated how gender, reproductive status, age, social context (group size), predation risk (distance to cover) and food abundance (grass height), affect vigilance and intake rate. The effect of these factors on the trade-off is indicated by the way they affect the slope of the relationship between intake and vigilance. We expected:

1. A decrease of intake rate with increases in vigilance [hypothesis (H1)].
2. No differences between males and females in their adjustment of intake rate with vigilance, since male and female zebras have similar basal energy/nutrient requirements as they have very little sexual dimorphism in body size (H2).
3. When investigating the two sides of the trade-off separately (i.e. vigilance or intake rate) and controlling for age and reproductive status, we predict that males should be more vigilant than females (H3a), as direct interference between males should require them to invest massively in monitoring rivals, and that intake in females should be higher on average than in males (H3b), as lactating females have higher energetic requirements.
4. For within-gender differences in the relationship between vigilance and intake rate, if the reproductive status shapes the adjustment of intake rate with vigilance, we expect a difference in the strength of the relationship according to both age and reproductive status within both sexes (H4).
5. When investigating vigilance and intake rate separately for the two genders, our main hypotheses are that stallions should be more vigilant than bachelors (H5a) because they should be scanning for predators as well as potentially cuckolding males [social vigilance, sensu Rubenstein (1986)], and lactating females should have higher intake rates than other adult females (H5b).
6. Finally, we expected zebras to increase their vigilance when close to cover (H6a) (as lions are ambush predators that generally remain in cover during the daytime), as well as in tall grass (H6b) (because of the decrease in visibility), and to increase their intake rate when foraging in taller grass (H6c).

Materials and methods

Study area and animals

The fieldwork was conducted in the Main Camp area of HNP in Southwestern Zimbabwe (19°00'S, 26°30'E), between March and July 2009, at the end of the wet season. Ecological conditions and especially grass availability and quality thus remained similar for the zebras during the whole period. The study site is an open grassland area of ca. 64 ha enclosed by *Acacia/Combretum* bushes, one of the plant communities characteristic of mixed bush grassland (Rogers 1993). Long-term mean annual rainfall is 606 mm, which mainly occurs during a rainy season from the end of October to the end of April (Chamaillé-Jammes et al. 2007).

Plains zebras are a gregarious species and form non-territorial harems consisting of a stallion, one or more female(s) (generally not more than four) and their foals (Klingel 1969). Young zebras disperse from the age of ca. 2 years: usually the young females join existing harems, and the young males join bachelor groups (Klingel 1969). The main predators of zebras in the study area are lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) (Drouet-Hoguet 2007; Loveridge et al. 2007).

Zebras were identified individually from their unique stripe patterns, and the population of Main Camp has been monitored since July 2004, with monitoring sessions every 6 months. For all sightings the characteristics of the individuals were noted, together with age class, reproductive status, family structure, and individual photos taken of both sides of each zebra, currently 320 individuals. This allowed us to separate males and females of different status with confidence. In this analysis, we determined for each individual the sex, age class (divided into two classes, sub-adult and young adult versus prime and older), reproductive status in males (bachelor versus stallion), and assessed if females were lactating (yes versus no, on the basis of observed suckling by their foal). The data on foals and yearlings were not analysed here, as no information was available to assess their intake rates.

Behavioural data

Behavioural data were collected by videotaping (Sony DCR-SR30 video camera, 20× optical) from vehicles, respecting a distance of ≥ 100 m between the focal group and the observer. The animals were habituated to vehicles and accepted them at 5–50 m. Animals were chosen at random for a 5-min focal sample, during the daytime. We considered groups whose predominant activity was foraging and which did not move far during the recording, ensuring that group size and composition did not change during the video sequence. Spatial groups were identified 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 all focal sampling [as in Frid (1997) for other mammals]. There were no ambiguities in defining a group using these criteria as inter-individual distances were very small. Group size was therefore taken as being equal to the size of the spatial group. According to Rubenstein and Hack's study (2004), our observed groups corresponded thus to harems with or without temporarily associated bachelors and bachelor groups.

Distance to cover ($D \leq 25$, $25 < D \leq 100$, $D > 100$ m) was estimated while filming. It is commonly used as a proxy for predation risk (Lima 1990; Burger et al. 2000; Blumstein et al. 2003). Since zebras use open areas, and as their main predator, the lion, is an ambush predator and spends the

daytime in cover, we assume that zebras perceive proximity to cover as risky (Fischhoff et al. 2007; Burkpile et al. 2013).

Visibility around foraging individuals provides direct information on obstructions to their vision (Whittingham et al. 2004; Pays et al. 2012). For example, it has been found in socially foraging birds that vigilance increases as visibility around them declines (Guillemain et al. 2001). We thus estimated the grass height of the patch in which the focal individual was foraging. Grass height also influences intake rate as biomass increases with grass height (Owen-Smith 2002). We considered grass to be ‘short’ when it was not above the focal zebra’s hooves and ‘tall’ when grass height reached the tibia, which is above the level of a zebra’s eyes when feeding.

We considered that an animal was ‘vigilant’ when it raised its head above the horizontal, scanning its surroundings, without moving its feet. No ambiguities were encountered in distinguishing a vigilant from a non-vigilant animal. We extracted from each sequence the total time spent in vigilance, the total number of vigilant acts, and the total number of bites taken by the individual. When grazers take a bite, they make jerky head movements which are easily recognizable. The recordings were sometimes viewed several times to be sure that the behaviour of the animals was noted accurately. Occasionally, for example if the animal turned its back to the camera, it was not possible to count the bites; in these cases ($n = 9$), these data were discarded when analysing variation of intake rates. From this data set the percentage time spent vigilant and foraging was computed as was the bite rate. In total, 118 focal samples were recorded (81 for males and 37 for females). From these 118 sequences, we recognized 47 different known zebras (15 males and 22 females). In the analyses we considered as random factors (see statistical analyses below) individual identity and also sequence identity (corresponding to the group filmed), since several zebras could be filmed during the same video sequence. Focusing on individuals differing by gender and state necessarily limits sample size, but the benefit of following focal, known individuals was an overriding consideration. Because the focal samples needed to be controlled for many environmental, phenotypic and behavioural categories, as described below, we favoured the quality of the data rather than the number of samples to ensure standardized metadata for all individuals. We did not include group identity as another random factor because we had avoided repeating observations on the same groups as far as possible, and individual identities were taken into account in the analyses.

Intake rate estimation

No data are available on intake rates as a function of bite rate in zebras. However, detailed information is available

for horses. Intake rates in large herbivores depend largely on buccal morphology, and horses and zebras are so similar that it is not always possible to know which species a skull belongs to (V. Eisenmann, personal communication 1994). We therefore used the experimental work of Fleurance et al. (2009) to estimate intake rates of zebras, using the results from horses of similar body mass to the zebras in our population. There are strong relationships between biomass (or grass height), bite rate and intake rate for grazers [Figs. 1, 2 in Spalinger and Hobbs (1992)], so we used only the data from horses biting at the same rates (0–50 bites min^{-1}) as the zebras in our study, and only results from grasses of the same height (2–50 cm) as those used by the zebras. The relationship between bite rate (x ; bite min^{-1}) and intake [y ; g dry matter (DM) min^{-1}] was quadratic ($y = -0.039x^2 + 2.050x$, $F_{2,20} = 18.14$, $P < 0.001$, $R^2 = 0.66$), with intake increasing up to ca. 25 bites min^{-1} and decreasing beyond this (see Electronic supporting information). We used this equation to calculate estimated intakes of the zebras from their bite rates extracted from the video sequences; since low intake occurs when bite rates are both very low and very high (see Electronic supporting information), we focus our analyses on intake rates and use bite rates to back up the analyses.

Data analyses

We used linear mixed-effects models, with the sequence number and the identity of the individual as random intercepts to take account of repeated measures on individuals and of filming several individuals of one group at the same time. The large number of continuous and categorical independent variables reduced the df in the statistical procedures, so we used the following procedure for model selection. To investigate how independent variables (x_k) affected the response variables [$w(x)$] (i.e. vigilance or intake rate), we started our selection by running a model including all simple effects only:

$$w(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k \quad (1)$$

where β_0 was the intercept and β_k the coefficient derived for each factor x_k . We then ran a similar model including one of the two-way interactions which was biologically relevant and interpretable in terms of mechanisms influencing vigilance or intake rate:

$$w(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k + \beta_{k+1} x_k x_{k+1} \quad (2)$$

where β_{k+1} was the coefficient derived for the interaction between the two variables x_k and x_{k+1} . We compared the models (Eqs. 1, 2) (keeping the same random effects) with a likelihood ratio test (i.e. deviance between two models tested with χ^2). All biologically relevant two-way interactions were tested with this procedure. We finally tested for

the effect of the independent variables by running the two models (Eq. 1 or Eq. 2) if two-way interactions were significant without the studied factor and testing for the deviance between the two models using a likelihood ratio test. We did not use standard backward selection to keep all variables that acted as controlling factors. We then extracted the coefficients derived for each significant factor by running a minimal model including only significant variables.

To achieve normality and homoscedasticity and to have linear relations between our variables in all statistical procedures, we log transformed the total time spent in vigilance and the group size. We tested for multicollinearity of variables using the variance inflation factor. All variance inflation factors were <2 , showing no evidence of multicollinearity between variables. All analyses were performed with the `lme` function of `nlme` package in R 2.15.3 (R Development Core Team 2013).

Vigilance

We studied the total time spent in vigilance instead of the proportion of time, as this provided better goodness of fit. All individuals were observed for 5-min sessions, so the total time and the proportion of time provide a similar representation of the time invested in vigilance by the zebras. As individuals were either foraging or vigilant during the 5-min sequences, any increase of vigilance leads to a decrease of foraging time (or inversely). We studied the difference in vigilance [$w(x)$] between males and females, thus including in our model sex, age class, $\log(\text{group size})$, distance to cover and grass height (x_k in Eq. 1). As reproductive status in both males and females was partly correlated with age, and was sex dependent, we did not include reproductive status in this procedure. The effect of reproductive status on vigilance was investigated in the following procedure investigating within-sex variation of vigilance. In males, we tested the effect of reproductive status on vigilance by contrasting males still in their natal group with bachelors and stallions. We included $\log(\text{group size})$, grass height and distance to cover as independent variables to control for any effects. In females, we restricted the analyses to adult females (>4 years of age), and tested for the effect of lactation (determined by observation of these known animals) contrasting lactating and non-lactating adult females and including the same independent variables as for the males.

Between-sex differences of intake rate and adjustment of intake rate with vigilance

We investigated the relationship between intake rate [$w(x)$] with x_l the log-transformed total time spent in vigilance

(see Eq. 1) and also included in our model x_2 , the square of the vigilance, as a supplementary fixed factor to test for a potential curvilinear effect. To test for any difference of adjustment between males and females, we included in the model the sex (x_3) of the individual and x_k , the $\log(\text{group size})$, distance to cover, grass height and age and tested whether the two-way interaction between sex and vigilance was significant (see Eq. 2). As vigilance could also interact with group size, distance to cover, grass height and age, we also tested for other two-way interactions involving vigilance and one of these listed factors. It is important to note here that this procedure allowed us to investigate both between-sex differences of the adjustment of intake with vigilance through the interaction sex \times vigilance (x_1x_3) and also the effect of other factors on intake rate through potential significant differences in the intercept of the relationship. As reproductive status in both males and females was partly correlated with age, and was sex dependent, we did not include reproductive status in this procedure.

Within-sex differences of intake rate and adjustment of intake rate with vigilance

In order to investigate the effect of reproductive status, a similar statistical procedure to the one described above was performed separately on adult males and females using the same categories as in the analyses on vigilance. Including the interaction reproductive status \times vigilance in the model [which also included $\log(\text{group size})$, distance to cover and grass height] allowed us to investigate differences of adjustment of intake rate with vigilance in males and females. Moreover, this procedure allowed us to investigate whether these factors influenced intake rates in both sexes.

Results

Total time spent in vigilance and intake rate

The zebras spent on average 10 % of their feeding time in vigilance, with a high variability between focal samples (range 1–52 % of the time); males spent on average (\pm SE) 31.8 ± 2.7 and females 26.0 ± 3.7 s of the 5-min focal sample being vigilant, which is significantly different (coefficient \pm SE = 0.168 ± 0.086 , $\chi_1^2 = 3.965$, $P = 0.047$; Fig. 1a). Foraging time was therefore 2.2 % lower in males compared with females. The log-transformed group size ($\chi_1^2 = 0.003$, $P = 0.956$), distance to cover ($\chi_2^2 = 1.197$, $P = 0.550$), grass height ($\chi_1^2 = 0.012$, $P = 0.912$), age class ($\chi_1^2 = 0.034$, $P = 0.853$) and the two-way interactions including sex ($\chi_1^2 < 2.285$, $P > 0.131$) did not affect the total time spent in vigilance significantly.

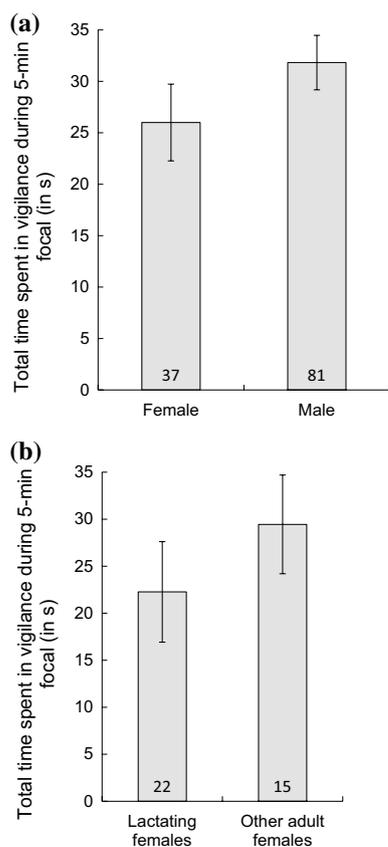


Fig. 1 Total time spent in vigilance during 5-min focal samples for male and female zebras (a) and for lactating and non-lactating adult females (b). Numbers of focal samples are indicated in each bar

Considering males only and controlling for the effect of the log-transformed group size ($\chi^2_1 = 0.017$, $P = 0.897$), distance to cover ($\chi^2_2 = 0.465$, $P = 0.793$), grass height ($\chi^2_1 = 0.580$, $P = 0.446$), we did not detect any significant effect of the reproductive status ($\chi^2_1 = 1.764$, $P = 0.189$). Thus, the levels of vigilance in stallions (31.5 ± 5.7 s) and bachelors (32.0 ± 2.8 s) were very similar. There was no significant effect on vigilance in males of the two-way interactions including the reproductive status ($\chi^2_1 < 6.383$, $P > 0.172$).

Considering adult females only and controlling for the effect of the log-transformed group size ($\chi^2_1 = 2.042$, $P = 0.153$), distance to cover ($\chi^2_2 = 1.210$, $P = 0.546$), grass height ($\chi^2_1 = 0.574$, $P = 0.449$), females in lactation spent 22.2 ± 5.3 s of the 5-min focal sample in vigilance, and were on average (\pm SE) less vigilant than other adult females (29.5 ± 5.2 s, coefficient \pm SE = -0.212 ± 0.091 , $\chi^2_1 = 3.869$, $P = 0.046$; Fig. 1b). No two-way interactions including the reproductive status of the adult females affected significantly the time they spent in vigilance ($\chi^2_1 < 1.084$, $P > 0.298$).

Between-sex differences in intake rate and adjustment of intake rate with vigilance

Intake during the 5-min focal sample was on average (\pm SE) 26.2 ± 0.4 g DM min^{-1} (Table 1). There was no significant difference between males (25.5 ± 0.5 g DM min^{-1}) and females (27.6 ± 0.5 g DM min^{-1}). The bite rates in males and females did not differ significantly either ($\chi^2_1 = 1.272$, $P = 0.259$). There was no significant effect of the two-way interactions between vigilance and gender, age, log-transformed group size, grass height or distance to cover (Table 1). Thus, individual zebras adjusted their intake rates with vigilance in similar ways, be they male or female (Fig. 2a). There was no significant effect of grass height, distance to cover and age class, but intake rate increased with group size (Table 1; Fig. 2d).

Within-sex differences of intake rate and adjustment of intake rate with vigilance

There was no significant effect of the two-way interactions between vigilance and reproductive status in males ($\chi^2_1 = 0.179$, $P = 0.672$), nor in adult females ($\chi^2_1 = 2.113$, $P = 0.348$), nor of any other factors including the log-transformed group size, grass height and distance to cover in both sexes ($P > 0.580$; Table 2). Thus we did not detect any difference in the decrease of intake rate with vigilance in males and adult females in relation to their reproductive status (Fig. 2b, c). However in males, while distance to cover ($\chi^2_2 = 1.319$, $P = 0.517$) and grass height ($\chi^2_1 = 0.139$, $P = 0.709$) did not affect their intake rate significantly, intake rate increased with group size ($\chi^2_1 = 5.544$, $P = 0.019$; see Table 2 for the positive sign of the coefficient). Intake was similar in stallions and bachelors (26.3 ± 0.8 , 24.8 ± 0.7 g DM min^{-1} , \pm SE) and did not differ significantly ($\chi^2_1 = 2.546$, $P = 0.111$); their bite rates were not significantly different either ($\chi^2_1 = 0.059$, $P = 0.808$).

In females the increase of intake rates with group size showed the same trend as in males, but was not significant ($\chi^2_1 = 2.730$, $P = 0.099$); their intake declined significantly with distance to cover ($\chi^2_2 = 7.248$, $P = 0.027$; Fig. 3a) and increased with grass height ($\chi^2_1 = 5.104$, $P = 0.024$; Fig. 3b). Intake rate was on average (\pm SE) 27.4 ± 1.0 in lactating and 26.9 ± 0.7 g DM min^{-1} in non-lactating females and did not differ significantly ($\chi^2_1 = 0.054$, $P = 0.816$), nor did their bite rates ($\chi^2_1 = 1.271$, $P = 0.260$).

Discussion

Decline of intake rate with the increase of vigilance

Both sexes spent little time in vigilance (<10 % of their foraging time). The low level of vigilance in these zebras

Table 1 Factors influencing the relationship between the log-transformed total time spent in vigilance and intake rate in zebras

Factors	χ^2	<i>df</i>	<i>P</i>	Coefficient \pm SE
Intercept				23.697 \pm 2.871 (<i>P</i> < 0.001)
Log(Vigilance)	31.410	1	<0.001	3.378 \pm 1.297
[Log(Vigilance)] ²	4.978	1	0.026	-3.345 \pm 1.707
Sex	1.125	1	0.289	
Age class	1.510	1	0.219	
Log(Group size)	7.705	1	0.006	6.301 \pm 2.146
Grass height	0.006	1	0.938	
Distance to cover	1.004	2	0.605	
Log(Vigilance) \times Sex	0.607	1	0.436	
Log(Vigilance) \times Age class	0.498	1	0.480	
Log(Vigilance) \times log(Group size)	2.426	1	0.119	
Log(Vigilance) \times Grass height	1.715	1	0.190	
Log(Vigilance) \times Distance to cover	2.497	2	0.287	

Coefficients (\pm SE) were extracted from a minimal model including only significant factors after likelihood ratio test model selection (see “Materials and methods” section for details). Individual identity and film sequence were included as random factors. Sex (female^a, male), age class (subadult and young adult^a, prime and senescent), distance to cover (*D* \leq 25, 25 < *D* \leq 100, *D* > 100 m^a) and grass height (short^a, tall) were considered as categorical

^a Levels used as the references in the model

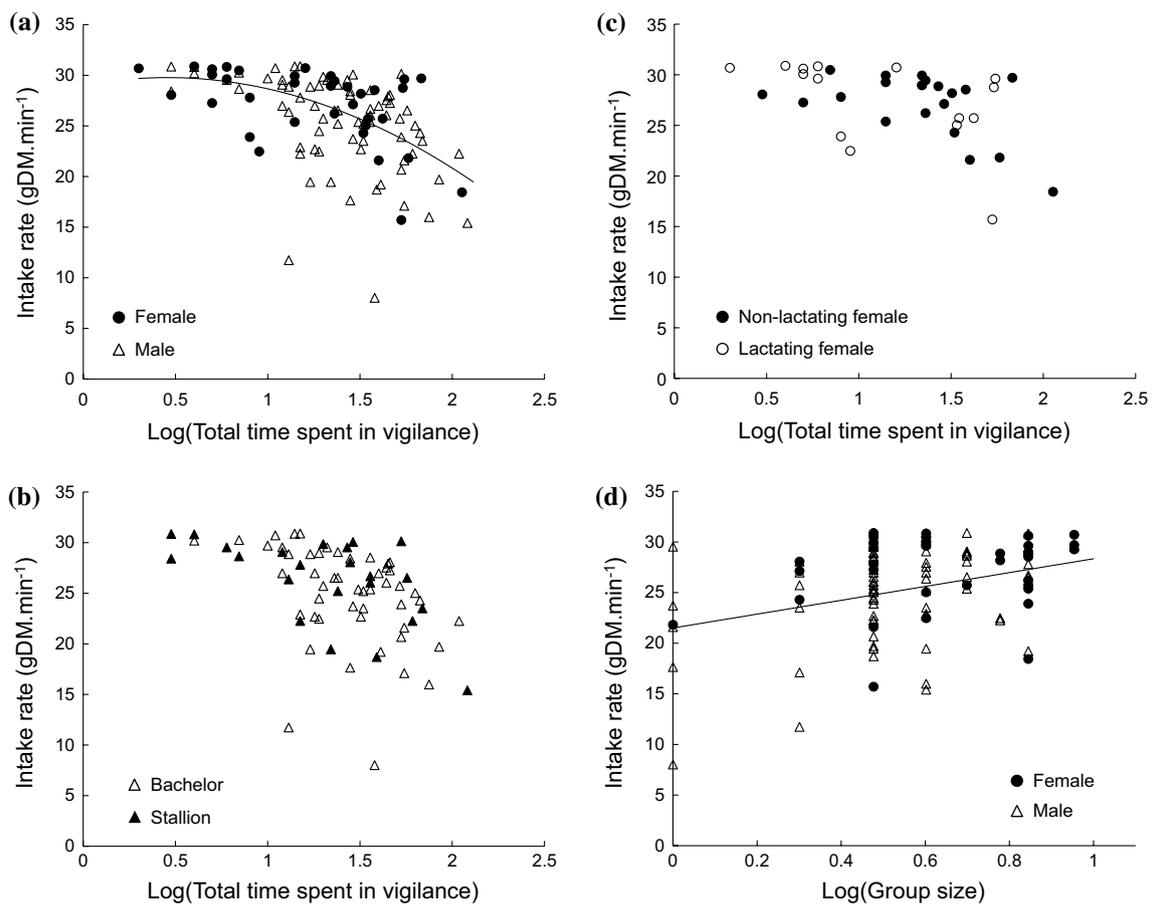


Fig. 2 Variations in the estimated intake rate (g dry matter min⁻¹) of zebras in relation to their vigilance in **a** males (triangles) and females (circles) and within sexes in relation to their reproductive status (**b**

males, **c** females); and **d** the increase in estimated intake rate in relation to the log-transformed group size. Fitted curves are derived from the model in Table 1

Table 2 Coefficients (\pm SE) of factors influencing the relationship between the log-transformed total time spent in vigilance and intake rate in adult male and female zebras

Variables	Males		Females		
	Coefficient \pm SE	<i>P</i>	Coefficient \pm SE	<i>P</i>	
Intercept	25.542 \pm 4.903	<0.001	29.513 \pm 2.265	<0.001	
Log(Vigilance)	8.492 \pm 3.100	<0.001	-4.321 \pm 1.338	<0.001	
[Log(Vigilance)] ²	-5.579 \pm 2.569	0.018		NS	
Reproductive status		NS		NS	
Group size	7.718 \pm 2.527	0.019		NS	
Distance to cover		NS	<i>D</i> \leq 25 m	4.995 \pm 1.852	0.015
			25 < <i>D</i> \leq 100 m	2.137 \pm 1.391	0.142
Grass height		NS	Tall	2.753 \pm 1.026	0.027
Estimated Intake \times Reproductive status		NS			NS

Coefficients were extracted from a minimal model including only significant factors after likelihood ratio test model selection (see “Materials and methods” section for details)

Individual identity and film sequence were included as random factors. Reproductive status (stallion, bachelor^a for males; lactating^a, non-lactating for females), *D* (*D* \leq 25, 25 < *D* \leq 100, *D* > 100 m^a) and grass height (short^a, tall) were considered as categorical

NS Non-significant

^a Levels used as the references in the model

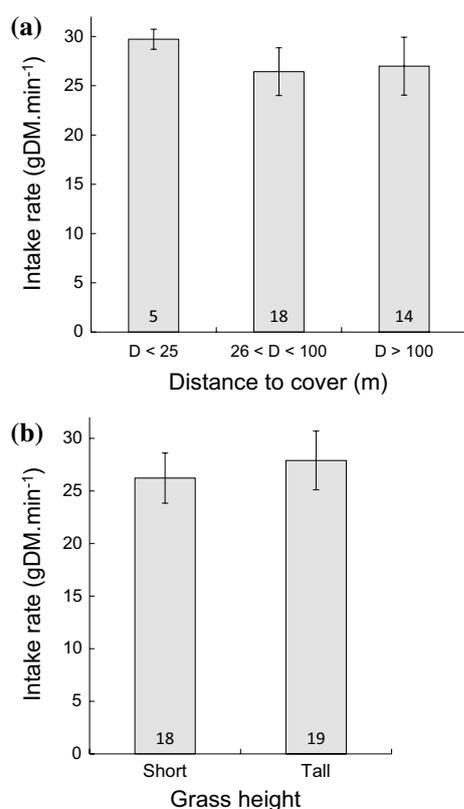


Fig. 3 Effect of distance to cover (a) and grass height (b) on the estimated intake rate (g dry matter min⁻¹) in female zebras of different age classes during 5-min focal samples. Number of focal samples is indicated in each bar

is surprising given the fact that this population appears to be limited by predation (Grange et al. 2015) and lions play an important role in determining their levels of vigilance (Péridet et al. 2012), and the quality of their diets [which is low, even in the wet season (Barnier et al. 2014)]. Free-living horses with no predators allocate about the same amount of time to vigilance as these zebras did [6–14 % of the 24 h (Duncan 1985)]. Zebras, like horses, face a strong time constraint on foraging time. They eat about 60 % more than grazing ruminants (Duncan et al. 1990), and have several functional reasons to allocate much of their time to feeding and restrict vigilance to a small proportion of their time: (1) their high intake feeding strategy leads them to spend ca. two-thirds of the 24 h feeding, with ca. 20 % of the time resting (Gakahu 1982), this leaves less than 25 % of the time for other activities like vigilance; (2) they forage on grass, and on the poor soils (Kalahari sands) of HNP, the quality of the grass is low (Rogers 1993). Hence, they are likely to need even more time for feeding here than in high-nutrient ecosystems (for the selection of high-quality items, and/or the achievement of high daily food intakes); (3) they are social foragers and inter-individual competition for access to high-quality patches is possible in a nutrient-poor savannah [see Blanchard et al. (2008) for impala *Aepyceros melampus* in HNP].

As expected (H1), intake decreased with increasing vigilance in both males and females, so the zebras traded food intake for vigilance (Fig. 1). A negative relationship between vigilance and feeding rate has been reported in many taxa

(e.g. Fritz et al. 2002; Cowlshaw et al. 2004), reflecting the potential intake cost of a high investment in vigilance. A negative relationship between vigilance and intake rate does not mean that individuals necessarily incur foraging costs of vigilance, as the cost depends on whether food intake actually declines. Many species of birds and mammals are able to time-share, by continuing food ingestion by handling or chewing their food during vigilance periods (Fortin et al. 2004; Blanchard and Fritz 2007; Unck et al. 2009; Pays et al. 2012), thus limiting the effective vigilance cost of foraging by maintaining an acceptable intake rate. This is especially true for herbivores (Spalinger and Hobbs 1992; Illius and FitzGibbon 1994). In HNP the great majority of observations of intake rates were above the minimum reported in horses of similar body size biting at the same rates and foraging in grasses of the same height [i.e. intake rates between 10 and 32 g DM min⁻¹ (Fleurance et al. 2009)]. This implies that these zebras, by avoiding a high investment in vigilance, appear to limit the associated costs of vigilance.

We could not distinguish vigilance for anti-predator purposes from vigilance for social purposes in this study. Social factors have been shown to influence levels of vigilance in several species (Favreau et al. 2010; Pays et al. 2012; Pappano et al. 2012) and could, as suggested by Simpson et al. (2012), be responsible for much of the vigilance shown by plains zebras, and horses: these are highly social animals.

Between-sex differences in intake rates and vigilance, and their trade-off

As predicted (H2), we detected no difference between males and female zebras in their adjustments of the instantaneous intake rate with vigilance. This supports the body-size hypothesis, which predicts a similar adjustment of intake rate with vigilance in species where males and females are sexually monomorphic.

As predicted (H3a), males were more vigilant than females [as is the case in many ungulates (see Prins and Iason 1989)]. The usual explanation is that direct interference between males requires them to invest time in monitoring rivals (Pays and Jarman 2008; Rubenstein and Hack 2004; Rubenstein 2010). However, no difference has been detected in some other mammals including African elephant *Loxodonta africana*, kob *Kobus kob*, impala (Burger and Gochfeld 1994), degu *Octodon degus* (Ebensperger et al. 2006) and in mixed-species troops of primates (Smith et al. 2004). Chamois females (*Rupicapra rupicapra*) tended to be more vigilant than males when they had young (Ferretti et al. 2014). It would be interesting in future studies to discriminate social and antipredator vigilance (as in Favreau et al. 2010) to understand better the processes involved in gender effects on vigilance, offspring care, inter-individual interference and/or predation risk.

In spite of the males spending less time foraging, we found no significant difference between the sexes in intake rates, contrary to H3b. Male zebras in the HNP population obtain food of poorer quality than females (Barnier et al. 2014), so it is likely that the poorer quality of their diet is a consequence of their allocation of more time to vigilance. Lactation often increases feeding rates in ungulates (e.g. Ruckstuhl et al. 2003; G elin et al. 2013), but in another monomorphic species, the chamois, males fed faster than females, but only in summer when they were greatly increasing their body reserves before the rut (Ferretti et al. 2014).

Within-sex differences in adjustments of vigilance with intake

Contrary to our prediction (H4) that reproductive status would affect the adjustment of intake to variations in vigilance, we did not detect any difference between individuals of different reproductive status in either males or females. In males, harem stallions were not more vigilant than bachelors (as opposed to H5a) and they did not differ in their intake rate either, presumably in trying to acquire females.

To compensate for the energetic demands of reproduction, it has been reported that mothers often increase food intake (J onsson 1997), and lactating females may increase their foraging time (Hamel and C ot e 2008) and/or forage more intensively (Cripps et al. 2011; Neuhaus and Ruckstuhl 2002). We had predicted an effect of reproductive status on intake rate in females (H5b), but did not detect any significant difference of intake rate between lactating and other adult females. As in males, the extra time spent in vigilance by non-lactating females resulted in only a small decrease in feeding time (2.7 % less), which led to a small and non-significant decline in intake and in bite rates between lactating and non-lactating females. Previous work of Neuhaus and Ruckstuhl (2002) on zebras found that bite rates in lactating females were higher than in non-lactating ones. However, bite rates in Neuhaus and Ruckstuhl's studies (2002) (around 45 bites min⁻¹) were twice as high as those observed in HNP (see Electronic supporting information), suggesting that ecological conditions (such as grass height and/or quality) in our study sites differed strongly, and might be responsible for this difference in results; further, predation pressure in HNP is higher than in Etosha, where Neuhaus and Ruckstuhl (2002) conducted their study (Grange and Duncan 2006; Appendix 1). Interestingly, another study did not find any significant effect of reproductive status on bite rates in another monomorphic species, the African oryx *Oryx gazella* (Ruckstuhl and Neuhaus 2009). Although we found no difference in intake rates between lactating and non-lactating female zebras, lactating females were less vigilant than other adult

females, increasing their time spent feeding. The hypothesis that animals would adjust their vigilance in response to the costs of reproduction is thus partly supported, but this hypothesis might not be true in all species, and should be tested on other species before seeking to draw general conclusions.

We expected zebras to increase their vigilance when their perception of predation risk increased, when they were close to cover (as lions generally remain in cover during the daytime) (H6a) or in tall grass (as visibility decreased). This was not the case; other studies have reported contrasting results, with either a decrease of vigilance when distance to cover increased (Burger et al. 2000) or an increase with distance to cover (Carrascal and Alonso 2006). As lions (the main predators) are more active at night, and zebras are more sensitive to the risk of predation at night in their habitat selection (Burkepile et al. 2013; Fischhoff et al. 2007), their perception of predation risk may be lower during the daytime. If so, the costs of vigilance will differ between night and day, and vigilance may serve different purposes during these two periods. Vigilance in zebras may be used mainly for social issues during the day and mainly for anti-predator vigilance during the night: if so, this could explain the why they are not more vigilant close to cover during the day.

Intake rates were higher when the females fed in tall grass, as predicted under H6c, even though the vegetation obstructs vigilance. Biomass is thus a major driver of intake rate in zebra females, as is generally the case in grazers (Owen-Smith 2002).

Finally, the zebras, especially males (see Table 2), increased their intake rates in larger groups. This highlights the advantage for prey to forage with conspecifics, particularly for predator detection (Pays et al. 2013) and/or to obtain information to locate richer patches (Courant and Fortin 2012) by monitoring conspecifics. This advantage may explain the existence of large herds of zebras, through the association of different herms reported in Rubenstein and Hack (2004), particularly if the population of zebras is limited by predation, as in HNP (Grange et al. 2015). While males reduced the foraging cost of vigilance in larger groups, females adjusted intake rate with risk associated with distance from cover. This pattern in females might appear counterintuitive if the biomass is not higher close to cover and predators are in bushes during the daytime. However, the data on mean group size (\pm SE) with distance to cover suggest that the zebras tended to form larger groups close to cover on the basis of inter-individual distance ($D < 25$ m, 6.2 ± 0.8 ; $26 < D < 100$ m, 5.3 ± 0.6 ; $D > 100$ m, 4.3 ± 0.5).

In this study we focused on individuals differing by gender and reproductive state: this necessarily limits sample size, but predicting the strength of the difference between the two sexes in their vigilance-food trade-off requires that reproductive status, age, predation risk, social context and food availability are controlled for. We therefore favoured the quality of the data rather than the number of hours of observation to ensure standardized metadata for all individuals. The results are based on a sample size of >100 , but even this is not large when broken down into different categories. The fact that each observation lasted 5 min could have introduced noise, concealing important effects: given the results obtained, this does not seem to have been a general problem.

In conclusion, group size and food biomass are major drivers of food intake rates in these animals, and gender and reproductive status are major drivers of vigilance, as expected. We show here, for the first time in a monomorphic animal, that although males and females have distinct vigilance and foraging strategies, they adjust their bite rates and food intake in similar ways when they increase the time spent in vigilance. Further studies on zebras and on other monomorphic species are needed to determine the generality of these results, and experimental manipulation of the perception of predation risk and of social factors is needed to understand the mechanisms underlying the patterns found here.

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Author contribution statement O. P. and H. F. conceived and designed the experiments. O. P., P. B., F. B. and P. D. conducted the fieldwork. F. B. and O. P. analysed the data. F. B., O. P. and P. D. wrote the manuscript. Other authors provided crucial editorial advice.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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