
Foraging efficiency and vigilance behaviour of impala: the influence of herd size and neighbour density

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Abstract

Group foraging can be beneficial for ungulates by decreasing the time required for vigilance, but it can also prove costly because of competition. To determine responses to gregarious behaviour, we studied foraging activity and vigilance of impala (*Aepyceros melampus*) near Kruger National Park, South Africa. We measured time spent foraging, vigilant, moving, grooming, engaging in social interactions and determined herd size and group distribution (i.e. density). We calculated accepted food abundance (AFA), food ingestion rate, steps per minute and percent vigilance for female, bachelor male and herd male impala. There was no relationship between herd size and vigilance, but vigilance decreased with increasing density ($t_{1,311} = 4.91$, $P < 0.0001$). Additionally, AFA decreased ($t_{1,61} = 5.96$, $P < 0.0001$) and steps per minute increased ($t_{1,311} = 14.38$, $P < 0.0001$) as more individuals fed in close proximity to each other. Impala could be altering their behaviour to accommodate a perceived change in resources because of intraspecific competition and these adjustments might be related more to the distribution of herd members than to herd size. Further studies should examine the behaviour of gregarious animals in relation to the distribution of herd members in addition to group size.

Key words: *Aepyceros melampus*, competition, gregarious, group foraging, predator avoidance, South Africa

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Résumé

Le fait de se nourrir en groupe peut être avantageux pour les ongulés parce qu'il réduit le temps nécessaire à la surveillance, mais il peut aussi se révéler coûteux en termes de compétition. Pour déterminer les réponses à un comportement grégaire, nous avons étudié l'action de se nourrir et la vigilance chez l'impala (*Aepyceros melampus*) près du Parc National Kruger, en Afrique du Sud. Nous avons mesuré le temps passé à se nourrir, à surveiller, à se déplacer, au toilettage, à l'engagement dans des interactions sociales, et nous avons déterminé la taille de la harde et la distribution du groupe (c.-à-d. sa densité). Nous avons calculé l'abondance de nourriture acceptée (AFA), le taux d'ingestion de nourriture (FIR), les pas par minute et le pourcentage de vigilance chez les femelles, les mâles célibataires et les impalas mâles en hardes. Il n'y avait pas de relation entre la taille de la harde et la vigilance, mais la vigilance diminuait lorsque la densité augmentait ($t_{1,311} = 4,91$, $P < 0,0001$). De plus, l'AFA diminuait ($t_{1,61} = 5,96$, $P < 0,0001$), et le nombre de pas par minute augmentait ($t_{1,311} = 14,38$, $P < 0,0001$) lorsque des individus plus nombreux se nourrissaient très près les uns des autres. Les impalas pouvaient modifier leur comportement pour s'adapter à la perception d'un changement des ressources dû à la compétition intraspécifique, et ces ajustements pourraient bien être liés plus à la distribution des membres de la harde qu'à sa taille. De nouvelles études devraient examiner le comportement des animaux grégaires en fonction de la distribution des membres de la harde, en plus de la taille du groupe.

Introduction

Vigilance, a main anti-predator strategy, can be costly for ungulates because it decreases time available for foraging

(Kie, 1999). Therefore, many ungulate species congregate and forage in groups (Jarman, 1974; Underwood, 1982; Kie, 1999). Although group foraging can be beneficial, disadvantages arise because of competition and mutual interference (Crawley, 1983). To cope with varying quantity and quality of forage, an herbivore adjusts its behaviour to meet necessary metabolic requirements, which can include altering forage selection and foraging rates (Owen-Smith, 1979).

Impala (*Aepyceros melampus* Lichtenstein, 1812) adjust their foraging decisions according to group size (Fritz & de Garine-Wichatitsky, 1996). With increasing group size, impala select browse on the basis of increasing the number of bites that could be taken from a particular bush (Fritz & de Garine-Wichatitsky, 1996). However, previous study conclusions were based on bush size and biomass only, not on specific foraging behaviour. Differences in biomass might be of little consequence to foraging efficiency, because an animal's foraging decisions also influence nutrient intake, physiology and ultimately the population (Owen-Smith, 1979). Additionally, herd distribution may affect feeding rates. We speculate that resource perception may decrease for animals feeding in higher concentrations because of an increased probability of experiencing intraspecific competition.

Two indices of foraging efficiency have been applied to studies on forage selection in impala (Dunham, 1982; Wronski, 2002, 2003); accepted food abundance (AFA), the ratio of feeding time achieved per unit distance covered and food ingestion rate (FIR), the proportion of foraging time devoted to feeding (Owen-Smith, 1979). Both indices reflected habitat and seasonal differences in food availability when applied to greater kudu (*Tragelaphus strepsiceros* Pallas, 1766) in Kruger National Park (Owen-Smith, 1979). In different vegetation communities and with seasonal environmental fluctuations, kudu decreased their AFA and FIR in response to decreasing forage quantity and quality (Owen-Smith, 1979). If an herbivore alters its foraging rate to cope with decreased food supply in various environments and across seasons, it might also alter its foraging rate because of a decrease in resources caused by intraspecific competition.

In addition to behavioural responses, group size and vigilance requirements can interact to affect foraging behaviour. Several studies report an inverse relationship between vigilance and group size in ungulates (Underwood, 1982; Prins & Iason, 1989; Illius & Fitzgibbon, 1994), but studies examining group size effects on

vigilance have demonstrated inconsistent relationships that depend on species, sex, habitat and other factors (e.g., age; Elgar, 1989; Bednekoff & Ritter, 1994; Burger & Gochfield, 1994; Shorrocks & Cockayne, 2005). For example, in Nairobi National Park, Kenya, only female impala exhibited the predicted inverse relationship between vigilance and herd size; territorial herd males and bachelor males showed no change in vigilance in response to group size (Shorrocks & Cockayne, 2005). Application of foraging indices would permit an additional evaluation of the vigilance-group size relationship and its effect on foraging efficiency.

We used AFA and FIR indices to examine potential changes in foraging efficiency and foraging rate in relation to number of potential intraspecific competitors by observing impala in various group sizes and concentrations. We also used these indices to evaluate vigilance behaviour in relation to group size, density and sex.

Materials and methods

Study area

This study was conducted at the Wits Rural Facility (WRF), located approximately 35-km from the Orpen Gate of Kruger National Park in the Limpopo Province, South Africa. The facility contains 350-ha of lowveld savannah dominated by *Terminalia sericea* Burch. ex DC., *Acacia* spp., and *Combretum* spp. Dominant grasses include *Panicum maximum* Jacq., *Pogonarthria squarrosa* Pilg., *Bothriochloa insculpta* (Hochst.) A. Camus, *Eragrostis gummiflua* Nees, *Aristida bipartita* Steud., and *Cynodon dactylon* (L.) Pers. (Shackelton, 1993). Mean annual rainfall is 670 mm, most of which is from October to April; mean annual temperature for the region is 22°C (Shackelton, 1993).

Large herbivores inhabiting the area include impala, common duiker (*Sylvicapra grimmia* Linnaeus, 1758), bushbuck (*Tragelaphus scriptus* Pallas, 1766), waterbuck (*Kobus ellipsiprymnus* Ogilby, 1833), reedbuck (*Redunca fulvorufula* Boddaert, 1785), greater kudu, and warthog (*Phacochoerus aethiopicus* Pallas, 1766). The study area generally lacks natural predators, although leopard (*Panthera pardus* Linnaeus, 1758) and spotted hyena (*Crocuta crocuta* Erxleben, 1777) have been occasionally observed. The facility is bordered on three sides by game reserves containing large predators which periodically enter the WRF (Geoffrey Craig-Cooper, WRF manager, personal communication).

Data collection

Methods used are similar to those of Owen-Smith (1979), Wronski (2002, 2003) and Dunham (1982). To investigate sex and social status effects on foraging and vigilance–group size relationships, we observed three classes of individuals: female, bachelor male and herd male. These individuals were distributed in bachelor and breeding herds. Bachelor herds contained male impala, including sub-adult males recently evicted from breeding herds. Breeding herds contained female impala with one territorial herd male. Occasionally, groups of females from the breeding herd were observed with the herd male absent. Observations of foraging and vigilance behaviour were made between 06:30–09:30 hours and 15:30–17:00 hours daily for 5 weeks during June and July 2007. We made detailed observations of three herds that were regularly observed at WRF: a breeding herd consisting of up to nineteen individuals and a bachelor herd of up to three individuals on the east end and an additional bachelor herd consisting of up to ten individuals on the west end. Because of movements and fragmentation between herds, group size varied between observations.

Impala were habituated to allow observations at a minimum of 25-m from a vehicle. We observed a focal individual for the amount of time required to take 50 steps or until it was no longer visible; behaviours were timed and categorized as: grazing, browsing, moving (>2 steps taken without feeding), standing alert (head raised and appearing to be scanning the surroundings), standing alert while chewing, grooming, social interactions and any other activities described accordingly. Each behaviour was recorded into a voice recorder and timed afterwards using a digital stopwatch. Feeding interruptions of less than 2 s were omitted, while interruptions lasting more than 2 min resulted in termination of the observation period and selection of another individual. To gauge an impala's response to competition, we recorded the number of animals feeding within an estimated 5-m radius of the focal individual in addition to group size. We used the term 'density' to distinguish this from herd size. If the density of individuals changed during the observation period, the mean number of individuals within 5-m of the focal animal was recorded.

Measurements of habitat structure were taken after impala left the area and included average tree (>2.5-m) and shrub (<2.5-m) height and percent cover within a 25-m radius of where the focal individual was first

observed. Average sward height and per cent grass cover were estimated within a 10-m radius. Visual obstruction measurements (VOMs) were also taken with a Robel pole (Robel *et al.*, 1970).

Vigilance was determined from the proportion of the observation period that the focal individual spent standing alert (including standing alert while chewing). The AFA was determined as the amount of time required for the individual to make 50 steps while foraging and FIR was calculated by dividing the amount of time spent feeding by the total time of the observation period (Owen-Smith, 1979). Only observations in which the focal individual took ≥ 50 steps were included in AFA calculations. To include all data points, AFA was converted to steps per minute, or steps taken divided by observation time. Observations where individuals moved more than ten steps without foraging were omitted from calculations of AFA, FIR or steps per minute. Observations were grouped by herd size and type, sex and density.

Data analysis

Statistical analyses were conducted using JMP Statistical Software v.7 (SAS, Cary, NC, U.S.A.), and data were log-transformed to allow for parametric testing. We used multiple-linear regression with standard least-squares to investigate the relationships between the response variables such as foraging and vigilance behaviour and the explanatory variables such as sex, herd size and density. Explanatory variables were included in the same model but considered separately. Additionally, herd size and density were evaluated by sex to infer gender-specific relationships. Because of the limited number of impala herds on the facility, it cannot be assumed that all observations are independent. Although steps were taken to avoid observing the same individual more than once per day, repeat observations of the same individual occurred over the entire study period. Therefore, the scope of this study was to provide a baseline reference on which inferences for longer-term studies with larger sample sizes could be made.

Results

A total of 334 observations were used in data analyses and 74 of the focal individuals took 50 steps (median steps per observation = 26). Range in observation time was 60–1171 s (mean = 315 s). Mean herd size of impala

observed during this study was eleven with mean density 3; impala during this study spent on average 82% of their time grazing, 1% browsing, 3% grooming, 1% engaged in social or other behaviours, 2% moving and 11% vigilant.

Accepted food abundance

Accepted food abundance varied by sex ($F_{2,73} = 3.3711$, $P = 0.0399$). Bachelor male impala exhibited the highest overall AFA (Fig. 1, $\bar{x} = 641.0$ s, 95% CI: 525.3–756.7), followed by herd males ($\bar{x} = 514.3$ s, 95% CI: 319.6–709.0) and females ($\bar{x} = 467.1$ s, 95% CI: 400.3–533.9).

There was no relationship between herd size and AFA (Fig. 2, $t_{1,61} = 0.14$, $P = 0.8894$). However, there was a negative relationship between AFA and density; AFA decreased by 68.7 s for every one-member increase in density ($t_{1,61} = 5.96$, $P < 0.0001$, 95% CI: -91.7 to -45.6). There was no correlation between grass cover ($t_{1,58} = 1.20$, $P = 0.2365$), height ($t_{1,58} = 0.05$,

$P = 0.9592$), or VOM ($t_{1,58} = 0.88$, $P = 0.3807$) and AFA.

These relationships were similar when AFAs were converted to steps per minute (Fig. 3). With every one-member increase in density, impala took 1.23 more steps per minute ($t_{1,311} = 14.38$, $P < 0.0001$, 95% CI: 1.06–1.39). Females took the most steps per minute ($\bar{x} = 7.40$, 95% CI: 6.85–7.94), followed by bachelor ($\bar{x} = 5.38$, 95% CI: 4.16–6.59) and herd males ($\bar{x} = 4.78$, 95% CI 3.02–6.53); $F_{1,333} = 8.5293$, $P = 0.0002$. This differs slightly from the results for AFA in that bachelor males exhibited the highest AFA, but herd males took the fewest steps per minute.

Vigilance

There was no relationship between herd size and vigilance (Fig. 4, $t_{1,311} = 1.52$, $P = 0.1302$), but vigilance levels differed among the three categories of impala

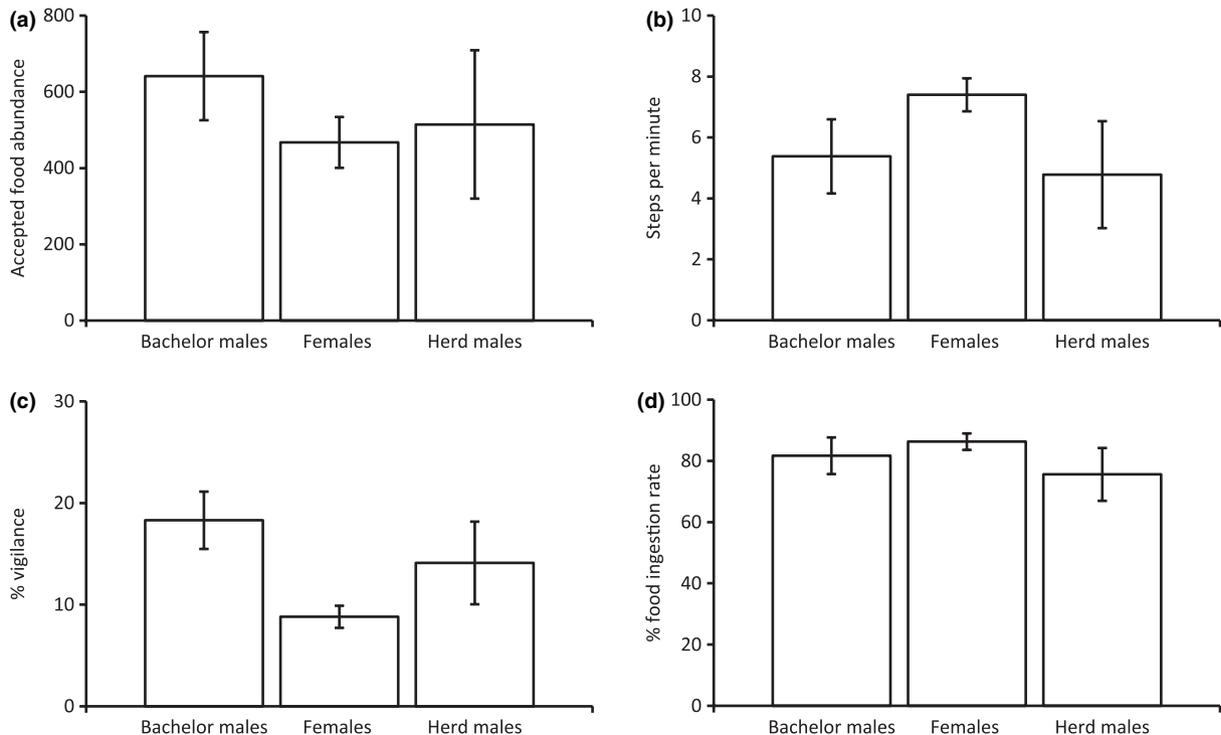


Fig 1 Average values and 95% upper and lower confidence limits. (a) Accepted food abundance for bachelor males ($\bar{x} = 641.0$ s, 95% CI: 525.3–756.7), females ($\bar{x} = 467.1$ s, 95% CI: 400.3–533.9), and herd males ($\bar{x} = 514.3$ s, 95% CI: 319.6–709.0), (b) steps per minute for bachelor males ($\bar{x} = 5.38$, 95% CI: 4.16–6.59), females ($\bar{x} = 7.40$, 95% CI: 6.85–7.94), and herd males ($\bar{x} = 4.78$, 95% CI 3.02–6.53), (c) % vigilance for bachelor males ($\bar{x} = 18.3\%$, 95% CI: 15.4–21.1), females ($\bar{x} = 8.8\%$, 95% CI: 7.7–10.2), and herd males ($\bar{x} = 14.1\%$, 95% CI: 10.1–18.2), and (d) % food ingestion rate for bachelor males ($\bar{x} = 75.6\%$, 95% CI: 69.6–81.6), females ($\bar{x} = 86.3\%$, 95% CI: 83.6–89.0), and herd males ($\bar{x} = 81.7\%$, 95% CI: 73.1–90.3)

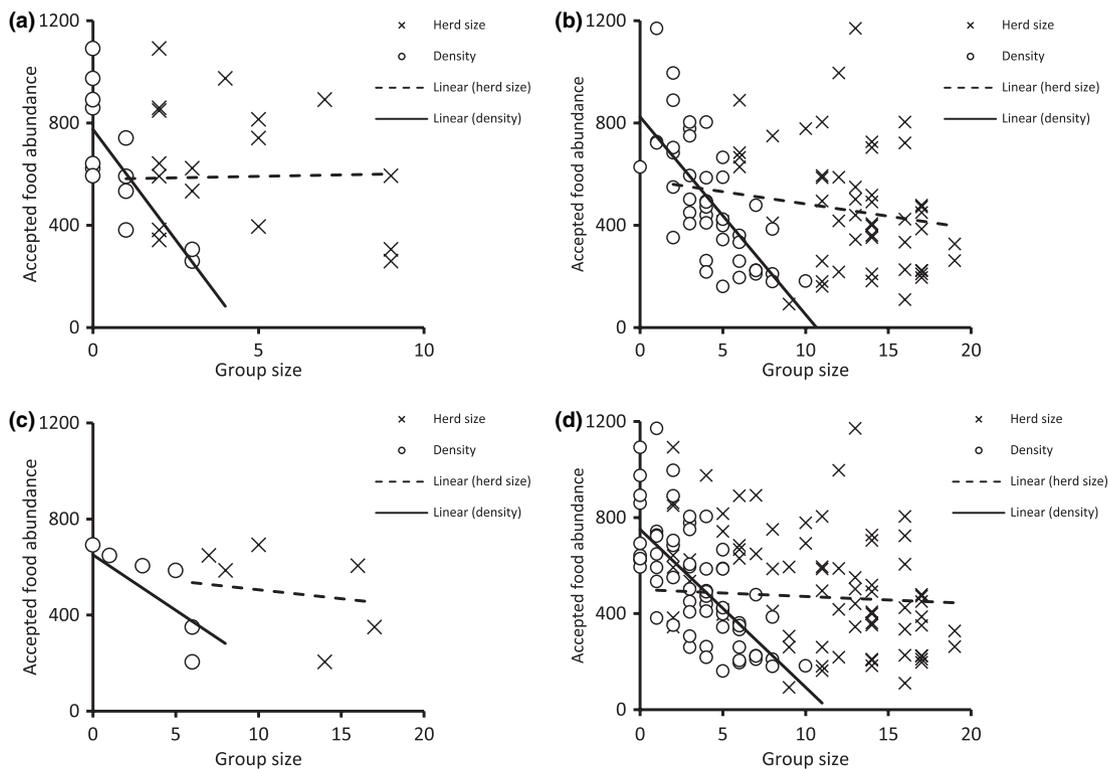


Fig 2 Accepted food abundance of foraging impala, (a) bachelor males in relation to herd size ($t_{1,10} = 0.05$, $P = 0.9603$) and density ($t_{1,10} = 3.32$, $P = 0.0077$), (b) females in relation to herd size ($t_{1,42} = 1.23$, $P = 0.2241$) and density ($t_{1,42} = 5.79$, $P < 0.0001$), (c) herd males in relation to herd size ($t_{1,5} = 0.56$, $P = 0.6148$) and density ($t_{1,5} = 2.04$, $P = 0.1344$), and (d) all impala in relation to herd size ($t_{1,61} = 0.14$, $P = 0.8894$) and density ($t_{1,61} = 5.96$, $P < 0.0001$)

($F_{2,333} = 15.3219$, $P < 0.0001$). Bachelor males were the most vigilant ($\bar{x} = 18.3\%$, 95% CI: 15.4–21.1), followed by herd males ($\bar{x} = 14.1\%$, 95% CI: 10.1–18.2) and females ($\bar{x} = 8.8\%$, 95% CI: 7.7–10.2). A negative relationship exists between vigilance levels and density ($t_{1,311} = 4.91$, $P < 0.0001$). For each one-member increase in density, vigilance levels decreased by 1.1% (95% CI: -1.61 to -0.59).

When broken down by sex, female vigilance decreased by only 0.62% for every one-member increase in density ($t_{1,243} = 3.06$, $P = 0.0024$, 95% CI: -1.15 to -0.09). Bachelor male vigilance decreased by 1.98% for every one-member increase in density, but high variability affected the P -value ($t_{1,40} = 1.01$, $P = 0.3209$, 95% CI: -5.87 to 1.90). Herd males exhibited the strongest relationship between vigilance and density; vigilance decreased by 2.43% for every one-member increase in density ($t_{1,22} = 3.92$, $P = 0.0007$, 95% CI: -3.99 to -0.88).

When analysed separately, shrub cover within a 25-m radius correlated with vigilance levels ($t_{1,319} = 1.90$,

$P = 0.0584$), but the focus of this study was to look at density and group size effects. When included with herd size and density, there was no relationship between shrub height ($t_{1,299} = 1.37$, $P = 0.1727$), tree height ($t_{1,299} = 0.03$, $P = 0.9741$) shrub cover ($t_{1,299} = 1.50$, $P = 0.1344$), or tree cover ($t_{1,299} = 0.58$, $P = 0.5642$) and vigilance.

Food ingestion rate

There was no relationship between FIR and herd size ($t_{1,311} = 1.30$, $P = 0.1943$) or density ($t_{1,311} = 1.09$, $P = 0.2745$). FIR varied by sex; females exhibited the highest FIR ($\bar{x} = 86.3\%$, 95% CI: 83.6–89.0) followed by herd ($\bar{x} = 81.7\%$, 95% CI: 73.1–90.3) and bachelor males ($\bar{x} = 75.6\%$, 95% CI: 69.6–81.6). When analysed by sex, a positive relationship exists between FIR and density for herd males only (Fig. 5, $t_{1,22} = 2.33$, $P = 0.0292$); FIR increased 1.01% for each one-member increase in density (95% CI: 0.15–4.34). FIR was negatively correlated with

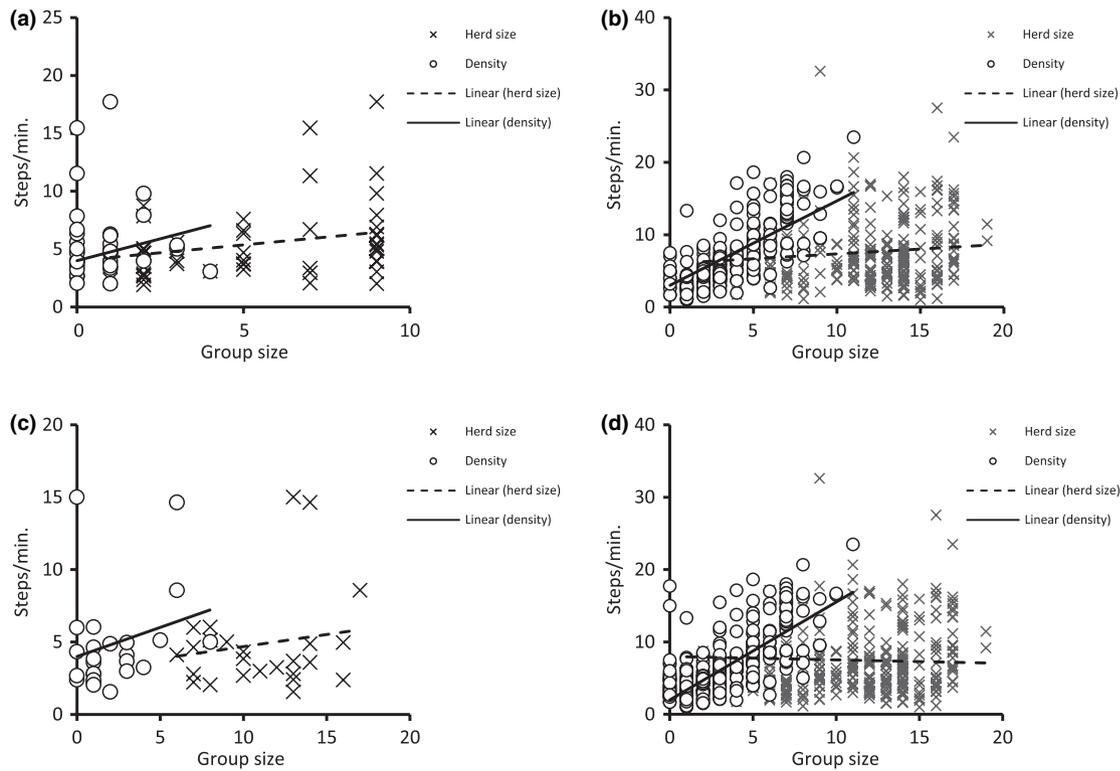


Fig 3 Steps per minute of foraging impala, (a) bachelor males in relation to herd size ($t_{1,40} = 2.27$, $P = 0.0288$) and density ($t_{1,40} = 2.00$, $P = 0.0528$), (b) females in relation to herd size ($t_{1,243} = 0.19$, $P = 0.8506$) and density ($t_{1,243} = 15.48$, $P < 0.0001$), (c) herd males in relation to herd size ($t_{1,22} = 0.53$, $P = 0.6046$) and density ($t_{1,22} = 1.62$, $P = 0.1197$), and (d) all impala in relation to herd size ($t_{1,311} = 0.43$, $P = 0.6708$) and density ($t_{1,311} = 14.38$, $P < 0.0001$)

vigilance, decreasing 0.53% for every 1% increase in vigilance (Fig. 6, $t_{1,332} = 12.12$, $P < 0.0001$, 95% CI: -0.75 to -0.32).

Discussion

Impala did not alter their foraging behaviour or vigilance in response to increasing herd size. However, AFAs were strongly influenced by density for all classes except herd males, indicating possible strong intraspecific competition. The sample size for herd males was smaller than that for bachelor males or females; a larger sample may yield different results. Along with decreased vigilance levels afforded by larger, clustered groups, competition and mutual interference are more likely to occur and thus require adjustment in foraging behaviour to meet nutritional requirements. A continuous source of forage afforded by grazing versus browsing would also yield lower AFA values. Low AFAs also suggest changing selectivity, as impala may be moving more

to eat the best forage before neighbouring group members. The decrease in AFA was not apparent with increasing herd size; it may be that higher interference caused by higher density may drive behavioural responses to intraspecific competition more than herd size.

Impala respond to greater densities of individuals because mutual interference and competition may elicit a resource perception response similar to seasonal variability in forage quantity. From a longer-term study of impala foraging behaviour in Zimbabwe, the feeding time achieved per 50 steps was at a maximum during the wet season and decreased sharply with the onset and progression of the dry season as resource availability decreased (Dunham, 1982). Similarly, AFA for kudu in Kruger National Park decreased during the mid dry season before rising again with new leaf flush in the wet season (Owen-Smith, 1979). Additionally, impala have shown to respond to larger group sizes by selecting browse based on available biomass (Fritz and de Garine-Wichatitsky, 1996).

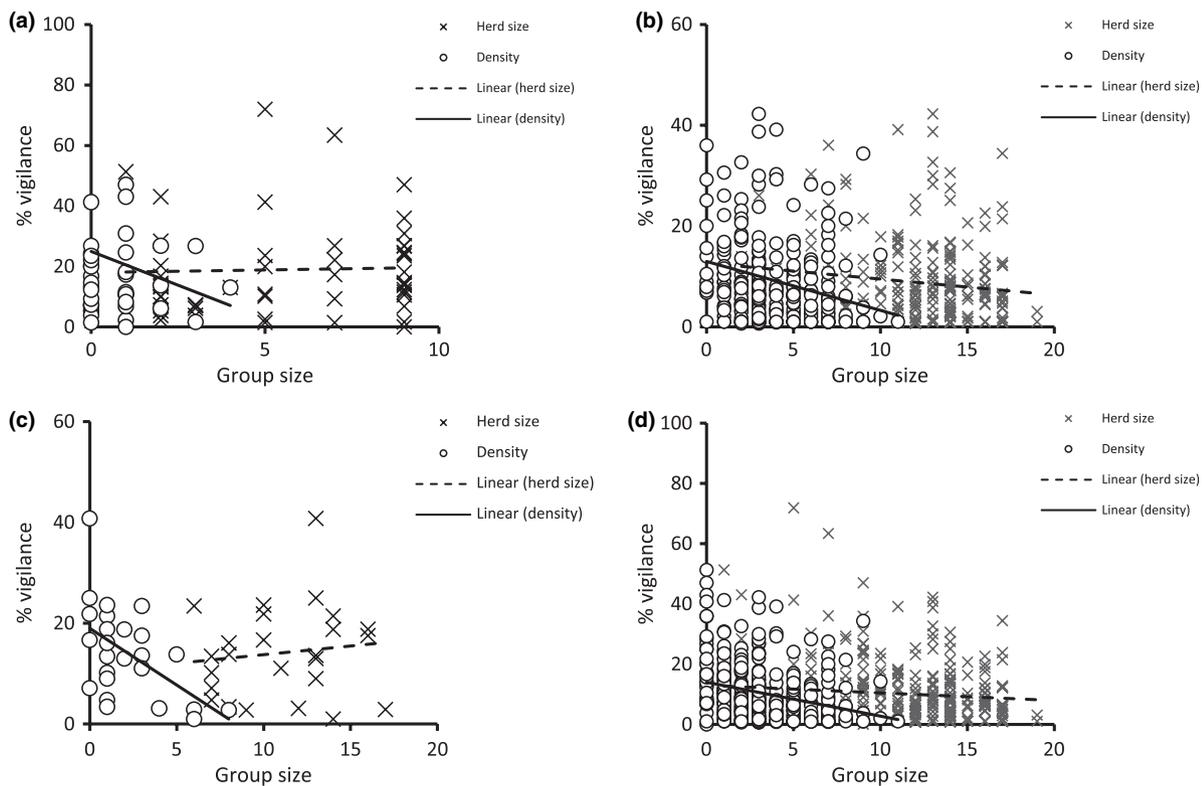


Fig 4 % Vigilance of foraging impala, (a) bachelor males in relation to herd size ($t_{1,40} = 1.12$, $P = 0.2678$) and density ($t_{1,40} = 1.01$, $P = 0.3209$), (b) females in relation to herd size ($t_{1,243} = 1.41$, $P = 0.1588$) and density ($t_{1,243} = 3.06$, $P = 0.0024$), (c) herd males in relation to herd size ($t_{1,22} = 0.84$, $P = 0.4101$) and density ($t_{1,22} = 3.92$, $P = 0.0007$) and (d) all impala in relation to herd size ($t_{1,311} = 1.52$, $P = 0.1302$) and density ($t_{1,311} = 4.91$, $P < 0.0001$)

There was no apparent relationship between FIR and either herd size or density, except for herd males, whose FIR increased with density. FIR decreased with increasing vigilance indicating that rate of food ingestion is impacted by vigilance. However, FIR did not increase to the same degree that vigilance decreased. There was a slight negative relationship between vigilance and time engaged in other activities (e.g. grooming and social interactions) suggesting that impala can dedicate time to other activities as vigilance decreases. An examination of FIR and daily activity budgets would provide more information about these relationships.

In both the Dunham (1982) and Owen-Smith (1979) studies, impala and kudu decreased their FIR (albeit at a lesser degree than AFA) with progression of the dry season. Impala and kudu in these studies browsed to a greater extent and movement between browse species would contribute to lower AFA and FIR values. In our study, forage availability remained constant (i.e. no seasonal

change) and impala mostly grazed (a continuous source of forage versus a patchier source with browse). Additionally, an assumption of both foraging indices is that the rate of food intake while foraging is constant (Owen-Smith, 1979). We did not examine bite size or bite rates in this study to determine if foraging rate was affected at this level; hence, if impala compensate for perceived competition by increasing the rate of food intake, this may be due to increased bite sizes or bite rates more so than increases in feeding time.

In our study, there was a no relationship between herd size and vigilance, which is inconsistent with Shorrocks & Cockayne (2005), who found that female impala vigilance decreased with herd size. However, their study included data from 38 impala with observation times ranging from 18 to 690 min, whereas our study included a total of 334 observations with shorter observation times ranging from 1 to 20 min. Furthermore, our study was restricted to peak foraging times, whereas Shorrocks & Cockayne (2005)

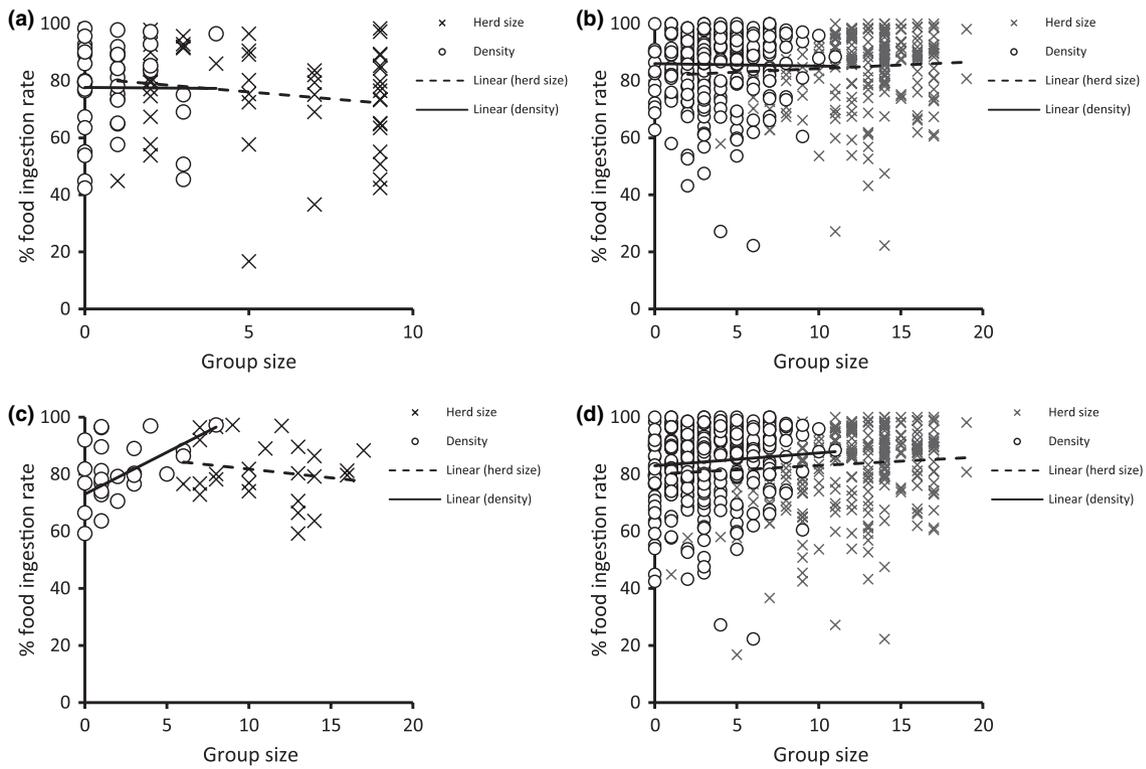


Fig 5 % Food ingestion rate of foraging impala, (a) bachelor males in relation to herd size ($t_{1,40} = 1.44, P = 0.1571$) and density ($t_{1,40} = 0.28, P = 0.7843$), (b) females in relation to herd size ($t_{1,243} = 1.29, P = 0.1994$) and density ($t_{1,243} = 0.19, P = 0.8483$), (c) herd males in relation to herd size ($t_{1,22} = 1.62, P = 0.1185$) and density ($t_{1,22} = 2.33, P = 0.0292$), and (d) all impala in relation to herd size ($t_{1,311} = 1.30, P = 0.1943$) and density ($t_{1,311} = 1.09, P = 0.2745$)

observed individuals throughout an entire day. Although our results provide useful inferences to impala behaviour during important foraging times, observation periods throughout the day may yield results more consistent with previous studies.

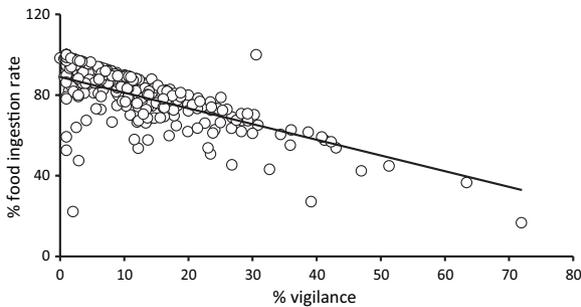


Fig 6 % Food ingestion rate of foraging impala in relation to % vigilance ($t_{1,332} = 12.12, P < 0.0001$)

Unlike herd size, which describes the total number of individuals in a group, density provides further information by conveying the distribution of the group. These measurements were useful in the study of impala vigilance, particularly concerning the herd male. Although there was no relationship between vigilance and herd size, the herd male decreased his vigilance levels as the number of females feeding nearby increased. Female impala are likely vigilant as a predator-avoidance strategy, whereas herd males must not only watch for predators, but also monitor females and watch for intruding males. The herd male is alone in this enterprise and his vigilance is thus independent of herd size (Shorrocks & Cockayne, 2005). If the herd male senses more females near him, he may be less inclined to be vigilant in monitoring their activity.

Additionally, FIR of the herd male increased with the number of females feeding near him; generally herd males spend less time foraging than bachelor males and females, and as a result have lower body condition (van Rooyen,

1993). If the herd male can afford lower vigilance levels at higher group densities, he may take advantage of these extended foraging opportunities. This would coincide with herd males having the lowest steps per minute and higher AFAs than females when modelled with density. Additionally, as low AFAs may imply changing selectivity, the herd male's higher AFA values, even when modelled with density, emphasize the importance of maximum food intake.

Vigilance of female and bachelor male impala decreased with density. Individuals in a group still need to be aware of other herd members. With more individuals feeding nearby, a female impala is aware of the herd's presence without having to look up. Although this decrease was not significant for bachelor males, they may be less vigilant for similar reasons.

Although the study area contained variable habitat types, locations where impala observations were made were similar in vegetation structure and visibility. Shrub and tree cover and height were irrelevant when included in the model with density. Vegetation and habitat type did not significantly affect impala vigilance in Nairobi National Park (Shorrocks & Cockayne, 2005). Food availability across habitat types and seasons affect an ungulate's foraging efficiency. VOMs taken with a Robel pole have been shown to correlate with standing crop measurements (Robel *et al.*, 1970); however, the basic vegetation measurements we made did not yield any relationships with AFA. Over a larger area across more variable habitats and multiple seasons, these measures may return different results.

The foraging indices, AFA and FIR, were effective in describing foraging behaviour of impala. Owen-Smith & Novellie (1982) predicted that an optimally foraging ungulate should widen its range of forage acceptance with declining food availability. This was documented for kudu in South Africa (Owen-Smith, 1979), impala in Zimbabwe (Dunham, 1982) and impala in our study. The pattern was similar albeit slightly different for impala in Uganda, a country which experiences a bimodal rather than unimodal rainfall pattern, thus affecting reproductive patterns and foraging behaviour to a lesser degree (Wronski, 2002). In all five studies, including ours, AFA was a more sensitive measure of foraging efficiency. The less noticeable FIR decrease in these studies was attributed to a seasonal extension of daily feeding time and an increased proportion of time devoted to other activities (Wronski, 2002).

The foraging indices reveal in some ways how an ungulate may adapt to varying group sizes and compensate for either a perceived decrease in resources caused by intraspecific competition or the need to sacrifice foraging time for vigilance behaviour. Both methods were applicable to foraging impala in this study area and the methodology was simple on a low budget and time-scale. Additionally, the foraging indices were useful in collecting data on vigilance behaviour, while simultaneously measuring foraging efficiency. Many studies on vigilance behaviour and group size consider only the number of individuals and not their density or distribution within that group. Despite the short-term period of this study, relationships linking density and distribution to vigilance and foraging behaviour became evident; assessing these variables on ungulate behaviour for a longer term study is needed.

Acknowledgements

We thank Geoffrey Craig-Cooper and Wayne Twine for providing assistance throughout the study, Prof. Norman Owen-Smith for providing a vehicle, staff at the WRF for logistic support, Dr Paul R. Krausman for financial support and Kerry Nicholson, Elizabeth LeRoux, Danielle O' Dell, Geoffrey Palmer and David Kahrs.

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(Manuscript accepted 21 June 2008)

doi: 10.1111/j.1365-2028.2008.01014.x