

# Vigilance behaviour and fitness consequences: comparing a solitary foraging and an obligate group-foraging mammal

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**Abstract** Vigilance behaviour in gregarious species has been studied extensively, especially the relationship between individual vigilance and group size, which is often negative. Relatively little is known about the effect of conspecifics on vigilance in non-obligate social species or the influence of sociality itself on antipredator tactics. We investigated predator avoidance behaviour in the yellow mongoose, *Cynictis penicillata*, a group-living solitary forager, and compared it with a sympatric group-living, group-foraging herpestid, the meerkat, *Suricata suricatta*. In yellow mongooses, the presence of conspecifics during foraging—an infrequent occurrence—reduced their foraging time and success and increased individual vigilance, contrary to the classical group-size effect. Comparing the two herpestids, sociality did not appear to affect overt

vigilance or survival rates but influenced general patterns of predator avoidance. Whereas meerkats relied on communal vigilance, costly vigilance postures, and auditory warnings against danger, yellow mongooses avoided predator detection by remaining close to safe refuges and increasing “low-cost” vigilance, which did not interfere with foraging. We suggest that foraging group size in herpestids is constrained by species-distinct vigilance patterns, in addition to habitat and prey preference.

**Keywords** Group foraging · Meerkats · Solitary foraging · Vigilance · Yellow mongoose

Virtually every tactic employed by a prey animal against predation is a trade-off between the positive and negative consequences of that behaviour. An individual that uses cover to shield itself against predator detection also reduces its ability to detect that same predator (Lima 1987; Lazarus and Symonds 1992) and may increase the probability of being attacked by ambush predators (e.g., Murray et al. 1995). Individuals grouping together may benefit from a greater number of alert eyes and prey individuals, allowing a decline in individual vigilance and increase in foraging time—the classical “group-size” effect (Elgar 1989; Quenette 1990). However, in larger groups, the increased potential for foraging competition, scrounging, and dominance interactions may force individuals to become more vigilant against conspecifics (Quenette 1990; Treves 2000), and larger groups may also suffer more frequent predation due to their increased conspicuousness (e.g., Caldwell 1986; Cresswell 1994). Whereas cooperation between group members could make flight responses more accurate through the use of functionally referential alarm calls (e.g., Seyfarth et al. 1980), socially facilitated predator detection could significantly increase the flightiness of

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cooperative species (Blumstein 2006), potentially reducing available foraging time.

As Beauchamp (2003) has pointed out, the expected pattern of vigilance changes in relation to group size and sociality are still unclear. As the majority of vigilance studies have focused on social foragers (Treves 2000), our understanding of antipredator responses in nongregarious species, especially, is limited. For example, the general assumption that solitary nocturnal primates rely primarily on crypsis for antipredator protection has only recently been shown to be an oversimplification of reality (Gursky and Nekaris 2007). Some interspecific studies (Tchabovsky et al. 2001b; Blumstein 2006) have tried to address the relative importance of environmental, social, and morphological factors on the wariness of gregarious and solitary animals. However, confounding factors such as habitat type and differential diets (Kaby and Lind 2003; Manaf et al. 2003) often make it difficult to isolate the effect of sociality itself on antipredator responses. Many questions thus remain concerning the interaction of social, predation, and other environmental effects on the antipredator tactics of prey animals. We studied antipredator behaviour in two sympatric, similar-sized species from the family Herpestidae, which fully overlap in their geographical distribution (Taylor and Meester 1993; Van Staaden 1994) to highlight the influence of sociality on their vigilance behaviour.

Within the family Herpestidae, group size is largely attributed to habitat and prey preference, and social structure ranges from obligate solitary to obligate social (Rood 1986; Veron et al. 2004). Diurnal, small-bodied herpestids that prefer open habitats and invertebrate prey—such as the meerkat, *Suricata suricatta*—live and forage mainly in groups, with a few notable exceptions, such as the yellow mongoose, *Cynictis penicillata* (Veron et al. 2004). The yellow mongoose belongs to the solitary clade of herpestids (Veron et al. 2004), although reproductive and social behaviours do not constrain denning group size—females are polyestrous (Rasa et al. 1992), and individuals in large kin groups (group size ranging from two to 13 members) display cooperative alloparental care (Balmforth 2004) and territory defence (Wenhold and Rasa 1994). Similar to other group-living solitary foragers (e.g., Schradin and Pillay 2004), the yellow mongoose primarily forages alone—occasionally in groups of two or three—across their distribution range (Nel and Kok 1999). The yellow mongoose emits alarm vocalisations when conspecifics are nearby, in particular, near the shared sleeping burrow (Earlé 1981; le Roux et al. 2008), but the occurrence of coordinated vigilance seems unlikely due to its mainly solitary foraging habits. Their diet, habitat, and predator suite—large raptors, medium-sized canids, and felids—overlap strongly with that of the obligate social meerkat (Lynch 1980). Meerkats live and forage in groups ranging from three to 50 members

(Clutton-Brock et al. 2002) and exhibit a range of cooperative behaviours from communal rearing and antipredator responses to teaching (Clutton-Brock et al. 2001; Manser 2001; Manser et al. 2001; Thornton and McAuliffe 2006). Similar to some other species (e.g., Wickler 1985; Horrocks and Hunte 1986), meerkats often have a sentinel watching out for predators (Clutton-Brock et al. 1999b; Manser 1999), and they have evolved a functionally referential alarm call system (Manser 2001).

The distinction between the foraging group sizes of the sympatric yellow mongooses and meerkats has been ascribed to differences in diet and microhabitat use (Avenant and Nel 1992; Rasa, cited by Nel and Kok 1999) and intraspecific foraging competition limiting foraging group size in yellow mongooses (Cavallini 1993). However, a study by Nel and Kok (1999) suggests that these three factors cannot conclusively explain why yellow mongooses remain solitary foragers—or at best, pair foragers—when their primarily invertebrate diet would place no constraint on group foraging. Citing “phylogenetic inertia”, the authors suggest that an unknown factor further back in their evolutionary history has placed an upper limit on the yellow mongoose’s foraging group size. Perhaps because meerkats and yellow mongooses have superficially similar antipredator tactics, i.e., guarding behaviour, vocal alarm signals, flight towards boltholes, and mobbing of predators (e.g., Manser et al. 2001; Graw and Manser 2007; le Roux et al. 2008), their antipredator behaviour has never been investigated as a possible constraint on foraging group size.

In this study, we examined how ecological and social factors affect vigilance behaviour and microhabitat use of a solitary forager and compare these tactics with an obligate group forager at a study site that is typical of both species’ preference for open habitats. In common with other small solitary mammals, we expected that yellow mongooses’ vigilance would be strongly affected by (a) their ecological environment, specifically, proximity to vegetative cover and safe refuges; (b) in keeping with the group-size effect, we expected that the presence of conspecifics would lead to a decrease in individual vigilance and, consequently, increased foraging time and success in yellow mongooses. For the social meerkats, we predicted that (c) individual vigilance and foraging success would be affected more strongly by social factors such as the proximity and vigilance of group members than by ecological factors. Comparing the two species, we predicted that (d) meerkats would devote less time to vigilance than yellow mongooses and would therefore have more time for foraging, as well as higher foraging success; and (e) they would differ in terms of microhabitat use—yellow mongooses staying closer to cover and safe refuges to counteract their lack of coordinated vigilance. Further-

more, we analysed life history data to compare survival rates of the two species.

## Materials and methods

We studied a wild population of yellow mongooses and meerkats at the Kuruman River Reserve (28°58'S, 21°49'E) in the Kalahari Desert, South Africa (Clutton-Brock et al. 1999a). The habitat here was representative of both species' preference for open habitats (Taylor and Meester 1993; Van Staaden 1994). On this reserve, yellow mongooses and meerkats used the same habitat and occasionally even shared sleeping burrows. For both species, the birth dates of most individuals were known, allowing us to accurately age focal animals. During the study period from February 2004 to March 2006, the average group size for yellow mongooses was  $3.7 \pm 0.4$  (mean  $\pm$  SE; range 2–7) for our nine focal groups, each consisting of the mated pair with their most recent offspring. This was the size of groups sharing a territory but differed from “foraging group” size, which was the focus of our study. Yellow mongooses were classified as foraging in a group when individuals foraged within a distance of 50 m from each other. At this distance, individuals were likely to see or hear each other's alarm signals—a raised tail or vocal alarm, given almost exclusively when individuals were in such a loose group (le Roux et al. 2008). Foraging groups consisted of one individual for 85% of active foraging time (le Roux et al. 2008) and varied between two and three individuals when yellow mongooses foraged in a group (15% of active foraging time). Pups below 2 months of age never went foraging with adults, as they remained at the sleeping burrow with a parent acting as babysitter (see also Balmforth 2004). Our data collection focused on adult yellow mongooses, which ranged between 641 and 668 g in body weight.

The six focal meerkat groups consisted of  $11.0 \pm 0.8$  members (ranging from 8–18). Meerkats denned and foraged together as a cohesive unit, resulting in the same group size for both contexts. Body weights for adult meerkats at this study site varied between 640 and 808 g (Clutton-Brock et al. 1999a). We focused only on subordinate adults in groups without foraging pups. This ensured that focal animals of both species were vulnerable to the same predator range, as neither yellow mongooses nor meerkats foraged with pups under 2 months of age. Predators such as martial eagles, *Polemaetus bellicosus*, black-backed jackals, *Canis mesomelas*, and Cape cobras, *Naja nivea*, were present on the reserve. These are known predators of both yellow mongooses (Taylor and Meester 1993) and meerkats

(Clutton-Brock et al. 1999a) and were encountered by meerkat groups at a rate of  $2.4 \pm 2.5$  aerial and  $0.8 \pm 1.1$  terrestrial predators per day (Hollén et al. 2008).

## Observations

We worked on habituated groups of yellow mongooses and meerkats, which allowed us to follow them closely without disrupting their natural foraging behaviour. Both species ignored our presence and did not show obvious signs of vigilance or fear towards the observer when followed at a distance of less than 5 m. We achieved habituation of 21 yellow mongooses (ten males and 11 females) through daily visits to sleeping burrows during 2004 (for more detail, see le Roux et al. 2008); whereas, meerkat groups had been studied since 1995 (Clutton-Brock et al. 1999a). Each individual yellow mongoose or meerkat group was typically observed only every second or third day either in the morning or in the afternoon (yellow mongooses only) for 2 to 4 h during foraging. Therefore, even if foraging and antipredator responses may have been affected by the potentially restrictive or protective presence of a human during observations, they were still exposed, unaccompanied by humans, to the full range of predators for more than half of their foraging time. Both species showed obvious responses to approaching predators in the presence of humans (Manser 2001; le Roux et al. 2008), indicating they did not rely on us as protection towards predators.

We conducted observations from January 2005 onwards during foraging periods, collecting focal and scan data (Altman 1974) on a handheld computer (Psion organiser II model LZ64) and spatial data on an eTrex (Garmin®) global positioning system. Scan data were noted every 5 min, and spatial location, every 10 min. These scan sessions were not interrupted during predator alerts. Focal observation sessions, lasting 20 min each, were opportunistically conducted if no predator had been spotted for at least 30 min beforehand and were paused whenever there was a predator alarm or if the focal animal was unseen for more than 5 s. We performed a total of 100 h of observations on adult yellow mongooses ( $N = 9$ ), collecting 188 sessions of scan data for solitary individuals and 17 sessions for yellow mongooses in foraging groups. We performed 67 focal observations on solitary yellow mongooses and 15 focal observations on individuals in foraging groups. For each focal meerkat, we conducted one morning session of scan and focal data collection, collecting a total of 36 h of data for 12 meerkats (six males and six females from six groups).

Data collection focused, firstly, on wariness, categorised as either “passive” or “active” vigilance. Passive vigilance, measured during scan intervals, implied an alert state that did not necessarily interrupt other activities. When an

animal's head pointed downwards, we considered it to be non-vigilant, in contrast to the vigilant states of a horizontal head position or an upwards-pointing head. We could ascertain the target of horizontal glances and classified these as non-vigilant when individuals were scanning for prey items. Active vigilance, measured during focal observations, was exhibited whenever a focal animal ceased other activities to visually scan the area for predators. We counted and measured the duration of three types of vigilance bout defined as bipedal guarding, while standing on the hind legs; quadrupedal guarding, while pausing on all four legs; and resting guarding, an alert state while sitting. In addition, we counted brief pauses—vigilant pauses in activity that lasted for less than 1 s. The average duration of brief pauses was determined as 0.838 s, based on the frame-by-frame analysis of six video recordings of focal animals in each species (filmed on a Sony HDR-HC3 4MP Handicam). An alarm response was defined as fleeing from a threat, usually accompanied by a vocal or visual alarm signal.

We described foraging behaviour by measuring the duration and number of foraging bouts during focal observations. A foraging bout started when an individual scratched at a foraging patch for longer than 2 s and ended when it moved to another patch or finished chewing a food item. We measured foraging success for each bout on a scale from 0 (no success) to 5 (extra-large item) depending on the size of the prey item and time taken to consume it (sensu Thornton 2008). The foraging success during a focal session was the combined successes for all bouts, reflecting the cumulative size of items consumed. Vigilance during foraging bouts was determined as the number of brief, alert interruptions to digging for food or eating, labelled as “foraging pauses”.

We described the social and ecological environment by noting proximity to vegetative cover (shrubs higher than 20 cm), boltholes (tunnels dug into the soft sand, serving as refuges to various small mammals), group members, and number of group members. Proximity to vegetative cover, in increasing order of safety, was categorised as out in the open, less than a body length away from cover, and under complete cover. Proximity to the nearest bolthole was classified as more than 10 m, between 5 and 10 m, between 2 and 5 m, and less than 2 m. Conspecific individuals within 50 m of the focal animal were regarded as group members.

#### Life history data

To investigate whether vigilance and foraging habits have an effect on survival, we calculated the survival rates of yellow mongoose and meerkat pups born between January 2004 and December 2006, as well as all the adults we

monitored. All known births and deaths of yellow mongooses were recorded. All sub-adult males and females disappeared from their natal territories between the age of 9 and 12 months. Nine of these individuals were found again, having established new territories (ALR, personal observation), and it was assumed that this was the age of dispersal for this population (compared with delayed dispersal in Balmforth 2004). If an individual “disappeared” while younger than 9 months, we presumed it dead. As the fate of most dispersing yellow mongooses was unknown, these individuals were excluded from calculations of adult survival rates. Data on births and deaths of meerkats for the same period were obtained from the long-term database of the Kalahari meerkat project comprising life history information for 15 habituated meerkat groups on the Kuruman River Reserve.

#### Statistics

##### *Vigilance and foraging behaviour*

All statistical analyses were done using R for Microsoft Windows version 2.3.1 (R Development Core Team 2006), using an alpha value of 0.05 as our threshold for significance. Yellow mongoose data were obtained according to a crossover design, as each individual was observed in multiple combinations of circumstances (p. 296 in Quinn and Keough 2002). This allowed us to analyse higher-order interactions of both focal and scan data using mixed-effect models with individual identity as a random variable and the relevant explanatory factors as ordered, fixed effects (Pinheiro and Bates 2000). Outcome variables were log-transformed where necessary to ensure the normal distribution of residuals. Assumptions of these models were checked using graphical analysis of residuals. We simplified saturated models by systematically removing interactions where *P* values were higher than 0.01 and main effects with *P* values higher than 0.05 (Crawley 2005). Non-significant main effects were retained if their interactions were significant.

Within-species analyses were conducted using two types of models to investigate the effect of several fixed factors on vigilance behaviour. For focal data, we used linear mixed-effect models with guarding duration and the number of guarding bouts as continuous outcome variables. We analysed scan data by means of generalised linear mixed-effect models with multivariate random effects, using a penalised quasi-likelihood approach (the *glmmPQL* function in R 2.3.1). These binomial models investigated the effect of fixed factors on the focal animal's head position—vigilant (pointing up or being level) versus non-vigilant (pointing downwards). The fixed factors we used in these mixed-effect models were (a) proximity to boltholes,

(b) presence and (c) guarding behaviour of group members, and (d) proximity to vegetative cover (only for scan data). In yellow mongooses, we also examined the effect of time of day (morning versus afternoon) on vigilance. In addition to these fixed factors, we incorporated (e) the presence of a sentinel, (f) distance to furthest group member, and (g) number of conspecifics within 5 m of the focal animal as fixed effects in models examining meerkat vigilance.

We compared the vigilance and foraging behaviour of yellow mongooses and meerkats. For each individual, we obtained the average number and duration of vigilance and foraging bouts and pauses, as well as foraging success during focal observations. Using scan data, we calculated the average proportion of observations in which head position was down, horizontal, or up. We compared active and passive vigilance and foraging behaviour between solitary yellow mongooses, yellow mongoose foraging in groups and meerkats using Kruskal–Wallis (KW) ANOVAs. Post hoc tests for significant differences were Mann–Whitney *U* tests. We calculated Cohen’s effect sizes for these nonparametric comparisons from simplified formulae in Quinn and Keough (p. 191, 2002) and Thalmeier and Cook (2002). As per convention, a “small” effect size is suggested by a Cohen’s *d* value between 0.20 and 0.49; a “medium” effect, between 0.50 and 0.79; whereas, a *d* value higher than 0.80 indicates a “large” effect size (Cohen 1992).

#### Microhabitat use

Based on scan observations, we calculated the average proportion of times each individual yellow mongoose and meerkat was observed at various distances from vegetative cover and boltholes. We used ArcView GIS animal movement extension (Hooge et al. 1999) to obtain average

speed of movement for each adult yellow mongoose and focal meerkat. We compared distance to vegetative cover and boltholes and speed between the species using KW ANOVAs and Mann–Whitney *U* tests.

## Results

### Vigilance and foraging behaviour

In yellow mongooses, active vigilance was affected only by proximity to a bolthole; whereas, passive vigilance was influenced by social factors as well as proximity to safe refuges. Contrary to expectation, guarding duration was shorter, and the number of brief pauses fewer, the further away an animal was from the safety of a bolthole (Table 1). The presence of group members did not affect active vigilance (linear mixed-effect model: all *P* values >0.05); whereas, time of day only affected the number of quadrupedal guarding bouts, which decreased in the afternoon. Passive vigilance increased when individuals were close to boltholes or when the focal animal foraged in a group but decreased when they were closer to vegetative cover (Table 2).

Active vigilance in meerkats was affected by the proximity of boltholes and certain social factors; whereas, passive vigilance was primarily affected by proximity to vegetative cover. Similar to yellow mongooses, vigilance increased closer to boltholes (Table 3). As the number of group members in close proximity rose, the duration of guarding behaviour—especially quadrupedal guarding—decreased. However, with a higher number of individuals in close proximity, focal animals increased overall guarding duration, if these group members were on bipedal guard. Increased proximity to vegetative cover was associated with

**Table 1** Significant effects from a linear mixed-effect model investigating nine measures of active vigilance calculated during focal observation sessions with yellow mongooses

Measure of vigilance	Parameter estimate±SE	denDF <sup>a</sup>	<i>F</i> value	<i>P</i> value
All guarding bouts (duration)	111.43 ± 41.94	157	13.3	<0.001
Quadrupedal guarding bouts (duration)	22.30 ± 8.02	157	7.72	0.006
Resting guarding bouts (duration)	73.42 ± 22.89	157	10.29	0.002
Brief pauses (count)	5.08 ± 2.43	157	4.38	0.038
Quadrupedal guarding bouts (count)	5.31 ± 1.87	156	8.35	0.004
Quadrupedal guarding bouts (count) <sup>b</sup>	−3.83 ± 1.87	156	4.21	0.041
Resting guarding bouts (count)	5.85 ± 1.62	157	13.13	<0.001

These measures of active vigilance were duration of resting, quadrupedal and bipedal guarding bouts; the number of brief pauses, resting, quadrupedal and bipedal guarding bouts; the total duration of all guarding bouts; and the total number of all guarding bouts. In all of these models, only the fixed factor “bolthole” (less than 2 m from focal animal) had an influence on vigilance, except where indicated

<sup>a</sup> Degrees of freedom for the denominator. Df for the nominator=1 in all cases

<sup>b</sup> Vigilance affected by time of day. Number of bouts decreased in the afternoon

**Table 2** Significant effects of various fixed factors on passive vigilance (head position) in the yellow mongoose

Fixed factor	<i>t</i> value <sup>a</sup>	<i>P</i> value	Odds ratio
Cover	-5.71	<0.001	0.5
Bolthole	2.27	0.025	1.13
Yno	8.98	<0.001	3.77

Degrees of freedom=195 for each factor. Cover: proximity to vegetative cover, bolthole: distance to nearest bolthole, yno: number of conspecifics within 50 m of the focal animal

<sup>a</sup> Positive *t* values indicate an increased probability for head position to be vigilant as the factor (putative safety) increases

decreased passive vigilance (glmmPQL:  $t_{56} = -1.98$ ,  $P = 0.05$ , odds ratio (OR) = 0.61); whereas, passive vigilance increased, not significantly, with a smaller distance between the focal animal and furthest group member ( $t_{270} = 1.81$ ,  $P = 0.07$ , OR = 1.62).

In terms of active vigilance, the two species differed in type of vigilance behaviour even though they spent an equal amount of time vigilant (Fig. 1a, two-tailed *t* test:  $t_{21,2} = -0.976$ ,  $P = 0.34$ ; Cohen's  $d = 0.59$ ). Whereas, quadrupedal vigilance ( $t_{21,3} = -3.56$ ,  $P = 0.002$ ; Cohen's  $d = 0.80$ ) and resting guard ( $t_{29} = -6.03$ ,  $P < 0.001$ ; Cohen's  $d = 1.15$ ) durations were much longer in yellow mongooses than meerkats, bipedal guards were more frequent—but not significantly so—in meerkats ( $t_{18,6} = 1.78$ ,  $P = 0.09$ ; Cohen's  $d = 0.37$ ) and were equal in duration ( $t_{17,3} = 0.588$ ,  $P = 0.56$ ; Cohen's  $d = 0.26$ ) between the species. Yellow mongooses had significantly more guarding bouts in total than did meerkats (Fig. 1b,  $t_{22,1} = -3.74$ ,  $P = 0.001$ ; Cohen's  $d = 0.82$ ). Fifty percent of these bouts were brief pauses, and the interspecific distinction can be attributed to a difference in number of brief pauses ( $t_{20,9} = -4.13$ ,  $P < 0.001$ ; Cohen's  $d = 0.87$ ), quadrupedal guards ( $t_{19,2} = -3.39$ ,  $P = 0.003$ ; Cohen's

$d = 0.97$ ) and resting guards ( $t_{29} = -5.62$ ,  $P < 0.001$ ; Cohen's  $d = 1.52$ ). The species further differed in how frequently they directed their gaze towards group members. Yellow mongooses looked at group members in 62 out of 644 guarding bouts. Meerkats looked at group members in ten out of 200 guarding bouts, paying less visual attention to conspecifics than did yellow mongooses (binomial test of proportions:  $\chi^2 = 3.62$ ,  $P = 0.06$ ).

The two species were distinct in terms of passive vigilance. Meerkats spent a larger proportion of their time looking down than yellow mongooses did (Fig. 1c, KW ANOVA:  $\chi^2 = 10.78$ ,  $P = 0.005$ ; Cohen's  $d = 0.73$ ); whereas, yellow mongooses spent more time with their heads held in a horizontal position (Fig. 1c, KW ANOVA:  $\chi^2 = 10.40$ ,  $P = 0.006$ ; Cohen's  $d = 0.78$ ). Post hoc tests indicated that the group and solitary values for yellow mongooses were similar to each other for both the head down ( $P = 0.807$ ) and horizontal head positions ( $P = 0.769$ ). Meerkats, however, differed significantly from yellow mongoose groups (head down:  $P = 0.001$ ; head horizontal:  $P = 0.001$ ) as well as solitary yellow mongooses (head down:  $P = 0.001$ ; head horizontal:  $P = 0.001$ ). Both species looked up less than 3% of the observational time (Fig. 1c, KW ANOVA:  $\chi^2 = 0.68$ ,  $P = 0.70$ ; Cohen's  $d = 0.50$ ).

The communal vigilance of meerkat groups was higher than that of yellow mongoose groups, but perhaps this may have been the reason for a large difference in number of predator alerts. The proportion of times that other group members were on guard was much higher for meerkats (119 out of 380 observations) than yellow mongooses (one out of 1,072 observations; binomial test of proportions:  $\chi^2 = 357$ ,  $P < 0.001$ ). Yellow mongooses (four out of 1,072 observations) interrupted foraging for alarm responses far less than meerkats (17 out of 380 observations;  $\chi^2 = 30.3$ ,  $P < 0.001$ ).

The comparison between the two species revealed few differences in terms of foraging behaviour or success.

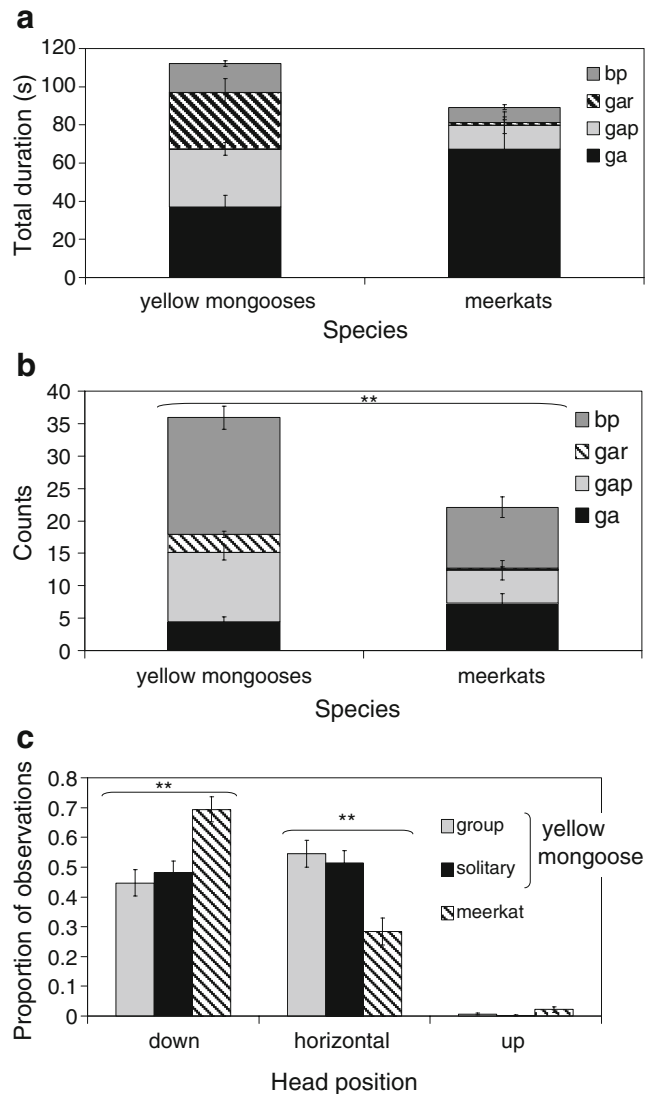
**Table 3** Significant effects of fixed factors on active vigilance in meerkats from mixed-effect models

Measure of vigilance	Factor	denDF <sup>a</sup>	Parameter estimate±SE	<i>F</i> value	<i>P</i> value
All guarding bouts (duration)	Bolthole	53	2.91 ± 0.39	55.24	<0.0001
	Yno	53	-0.71 ± 0.12	24.73	<0.0001
	Yga	53	-2.58 ± 0.93	0.20	0.661
	Yno:yga	53	0.82 ± 0.26	10.33	0.002
Bipedal guard (duration)	Bolthole	56	2.10 ± 0.42	24.78	<0.0001
Quadrupedal guard (duration)	Bolthole	55	1.25 ± 0.32	14.03	<0.001
	Yno	55	-0.17 ± 0.08	4.01	0.050
Brief pauses (count)	Bolthole	51	0.56 ± 0.26	2.94	0.093
	Yno	51	-0.22 ± 0.07	9.18	0.004

Bolthole: distance to nearest bolthole, yga: other group members on guard, yno: number of group members within 50 m of the focal animal

<sup>a</sup> Degrees of freedom for the denominator. Df for the nominator=1 in all cases

Yellow mongooses (solitary:  $15.55 \pm 2.38$  s, group:  $10.81 \pm 1.41$  s) foraged for shorter periods than meerkats, but this difference was not significant (duration:  $22.36 \pm 8.24$  s, KW ANOVA:  $\chi^2 = 5.63$ ,  $P = 0.06$ ; Cohen's  $d = 0.17$ ). Foraging success was similar between yellow mongooses (solitary:  $12.63 \pm 1.34$ , group:  $11.52 \pm 2.23$ ) and meerkats ( $9.62 \pm 1.62$ , KW ANOVA:  $\chi^2 = 2.15$ ,  $P = 0.34$ ; Cohen's  $d = 0.39$ ), as was the number of foraging pauses per focal observation session (solitary:  $0.57 \pm 0.09$ , group:  $0.74 \pm 0.20$ , meerkats:  $1.25 \pm 0.85$ , KW ANOVA:  $\chi^2 = 0.60$ ,  $P = 0.74$ ; Cohen's  $d = 0.36$ ).



**Fig. 1** **a** Duration (mean $\pm$ SE) and **(b)** number (mean $\pm$ SE) of active vigilance bouts per 20-min focal compared between yellow mongooses and meerkats. *Bp* brief pauses, *gar* resting guard, *gap* quadrupedal guard, *ga* bipedal guard. Yellow mongoose group and solitary data were combined, as there was no effect of group size on active vigilance (Table 1). **c** Passive vigilance (head position) compared between yellow mongoose groups, solitary yellow mongooses, and meerkats. Yellow mongoose group and solitary data separate due to effect of group size on passive vigilance (Table 2; \*\* $P < 0.01$ )

## Microhabitat use

The two species differed in their microhabitat use, with yellow mongooses being closer to safety more often than meerkats and moving at a comparatively higher speed. Yellow mongooses spent more time than meerkats under complete cover (Fig. 2a, KW ANOVA:  $\chi^2 = 10.73$ ,  $P = 0.005$ ; Cohen's  $d = 0.45$ ) but equal time close to cover (Fig. 2a,  $\chi^2 = 2.13$ ,  $P = 0.35$ ; Cohen's  $d = 0.39$ ) and in the open ( $\chi^2 = 0.37$ ,  $P = 0.83$ ; Cohen's  $d = 0.33$ ).

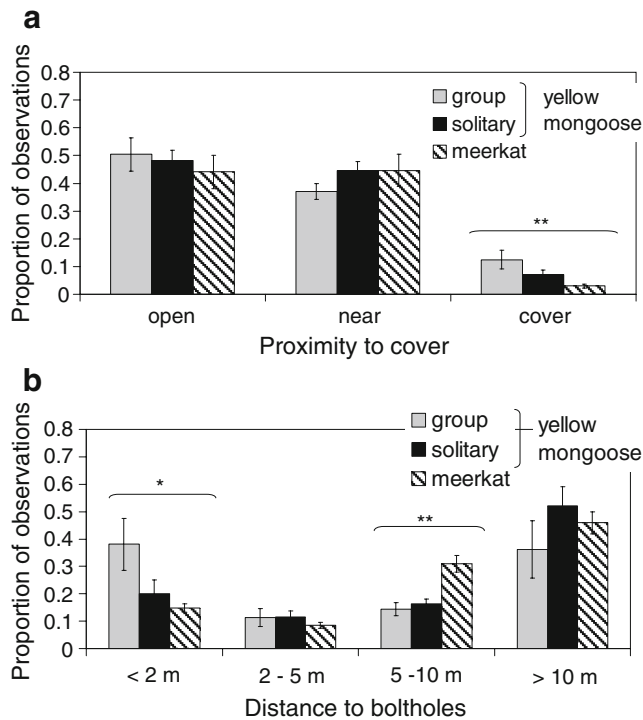
Yellow mongooses were more often within 2 m of a bolthole (Fig. 2b,  $\chi^2 = 5.99$ ,  $P = 0.05$ ; Cohen's  $d = 0.30$ ) but spent less time than meerkats between 5 and 10 m from boltholes (Fig. 2b,  $\chi^2 = 11.49$ ,  $P = 0.003$ ; Cohen's  $d = 0.65$ ). According to post hoc tests, yellow mongooses and meerkats did not spend a significantly different proportion of time within 2 m of a bolthole (yellow mongoose group versus solitary:  $P = 0.696$ ; yellow mongoose group versus meerkat:  $P = 0.085$ ; solitary yellow mongoose versus meerkat:  $P = 0.074$ ). However, whereas yellow mongoose groups and solitary yellow mongooses spent a similar proportion of time between 5 and 10 m from a bolthole (post hoc test:  $P = 0.865$ ), yellow mongoose groups ( $P = 0.001$ ) and solitary yellow mongooses ( $P = 0.003$ ) spent significantly less time than meerkats at this distance from boltholes. Yellow mongooses moved faster ( $0.13 \pm 0.01$  m/s) than meerkats ( $0.08 \pm 0.01$  m/s, two-tailed  $t$  test:  $t_{16,0} = -4.95$ ,  $P < 0.001$ ).

## Life history

There was a large interspecific difference in the absolute numbers of adults monitored and pups born during our study period (Fig. 3a), but the proportion of surviving individuals was similar for both species (Fig. 3b). Comparing yellow mongooses with meerkats, survival rates of individuals younger than 6 months (Fig. 3b, binomial test of proportions:  $\chi^2_1 = 0.80$ ,  $P = 0.37$ ), between 6 months and 1 year ( $\chi^2_1 = 0.08$ ,  $P = 0.78$ ), and older than 1 year (Fig. 3b,  $\chi^2_1 = 1.66$ ,  $P = 0.20$ ) did not differ. Individuals younger than 1 year were more likely to survive in yellow mongooses ( $\chi^2_2 = 11.66$ ,  $P = 0.003$ ), and meerkats showed a similar pattern of survival ( $\chi^2_2 = 5.01$ ,  $P = 0.082$ ).

## Discussion

Patterns of vigilance behaviour differed markedly between the solitary foraging yellow mongooses and the obligate group-foraging meerkats. Yellow mongooses held their heads in a horizontal position and moved fast in a stop-start pattern of locomotion, similar to other small mammals such as grey squirrels, *Sciurus carolinensis*, and eastern chipmunks, *Tamias striatus* (McAdam and Kramer 1998).

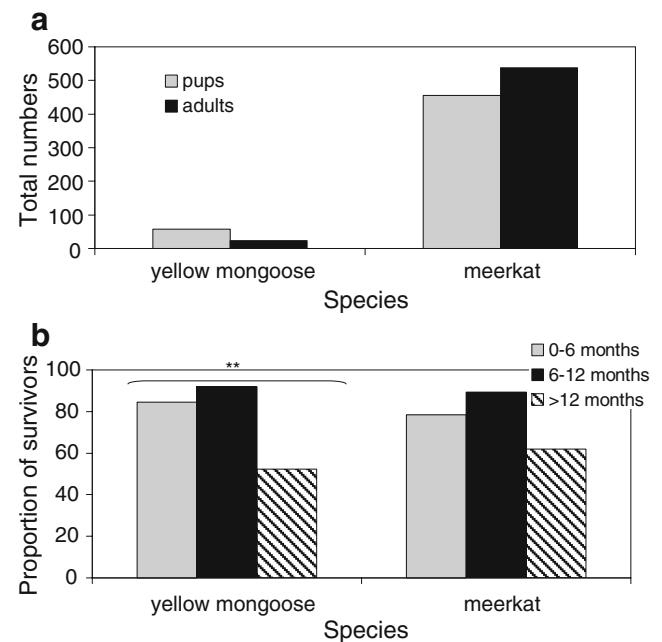


**Fig. 2** Microhabitat characteristics (mean proportion $\pm$ SE) compared between yellow mongoose groups, solitary yellow mongooses, and meerkat groups (\* $P=0.05$ , \*\* $P<0.01$ ). **a** Proximity to vegetative cover (open: more than a body length away from cover, near: within a body length from cover, and cover: completely under cover). **b** Proximity to boltholes

Such short, multiple pauses increase the likelihood of detecting predators by stabilising the visual field (Kramer and McLaughlin 2001), yet the high, intermittent activity levels of yellow mongooses may also draw the attention of raptors (sensu Snyder 1975) in a way that the slow, continuous movements of meerkats would not. In contrast to yellow mongooses, meerkats foraged with their heads down and, when vigilant, used vigilance postures such as bipedal guarding or acting as a sentinel (Manser 1999) that are costly in terms of foraging time. However, with at least one group member on bipedal guard 30% of the time (this study), coordinated vigilance, and functionally referential alarm calling (Manser 1999, 2001), individual meerkats are able to be less vigilant than yellow mongooses, which lack these cooperative antipredator responses. The head-down foraging behaviour of meerkats is likely to favour the discovery of the rarer items in their diet—viz scorpions of the genera *Parabuthus* and *Opisthophthalmus* (Doolan and MacDonald 1996)—that are detected by careful visual or palpating detection (Glaser 2006). However, the high vigilance levels of yellow mongooses did not detract from their foraging success, thus confirming the prediction of Illius and Fitzgibbon (1994) that vigilance does not conform to

the group-size effect when foraging and vigilance are not mutually exclusive behaviours.

For about half their foraging time, yellow mongooses and meerkats remained close to vegetative cover, similar to other small mammals (e.g., Lagos et al. 1995; Tchabovsky et al. 2001a). This proximity to cover probably reduced their visibility to predators in this habitat, although terrestrial ambush hunters (e.g., Murray et al. 1995) could make vegetation a potential source of danger. Both prey species were also likely to detect predatory threats more easily while out in the open, away from obstructive cover (sensu Lima 1987). The relatively equal amount of time spent near cover and out in the open—by both meerkats and yellow mongooses—may therefore have reflected this trade-off between the need to detect and to escape detection. In other small mammals such as spiny rats of the genus *Trinomys* (Manaf et al. 2003), solitary species make more use than social species of habitat features to increase safety. This was also seen in our study, as yellow mongooses stayed closer to boltholes than did meerkats and spent more time under complete cover. As shown by Blaum et al. (2007), yellow mongooses also show a strong preference for dens with good vegetative cover, even though their foraging areas are not densely vegetated. Crypsis appears to be an important part of yellow mongooses' antipredator behaviour, as they relied mostly



**Fig. 3** Fitness data of yellow mongooses and meerkats in the same area over the same 2-year period. **a** Absolute number of individuals born and adults monitored. **b** Survival rates at different ages (indicated in legend). Differences between species were not significant for any age class. Yellow mongoose survival rates differed between age classes (\*\* $P<0.01$ )



on inconspicuous vigilance postures (quadrupedal and bipedal vigilance), proximity to vegetation, and boltholes. This may be one reason why additional group members caused an increase in individual vigilance for yellow mongooses—foraging pairs and groups are more conspicuous and thus more vulnerable than solitary individuals.

In both species, vigilance behaviour was affected by the behaviour and presence of group members, but in opposite directions. In meerkats, individual vigilance decreased when other group members were on guard (see also Manser 1999) or close by, and in keeping with the group-size effect, an increase in group size leads to lowered active vigilance in individuals (Clutton-Brock et al. 1999a). Contrary to the group-size effect, yellow mongooses increased passive vigilance and experienced decreased foraging success as individuals went from a solitary to group-foraging state. Yellow mongooses also stayed much closer to boltholes when in a group. Their heightened vigilance is probably not due to the mimicking of vigilant group members—as found in, for example, wild boars, *Sus scrofa* (Quenette and Gerard 1992)—as the vigilance behaviour of conspecifics did not affect the alertness of yellow mongooses. Whereas, greater numbers and increased conspicuousness may have raised individual vigilance levels, foraging competition may be another reason (Gorman 1979; Cavallini 1993). However, our observations on foraging behaviour confirm the argument by Nel and Kok (1999) that foraging competition is likely to play a small role in constraining the size of yellow mongoose foraging groups, as the diet of yellow mongooses primarily comprises of invertebrates. During 900 h of observation, less than 0.2% of all foraging bouts were attempts to catch vertebrate prey—barking geckos, *Ptenopus garrulus*, and young pied babbler, *Turdoides bicolor* (N. Rhaiani, personal observation).

The qualitatively different vigilance strategies used by the sympatric yellow mongooses and meerkats did not have an influence on their comparative survival rate. Yellow mongoose and meerkat pups had an equal chance of reaching adulthood. Yellow mongoose pups appear to benefit from being fed at the sleeping burrow until they are large enough to fall out of the prey range of a number of raptors (Rasa et al. 1992) and forage by themselves. In contrast, meerkat pups forage with their group from an early age, where they are protected by the cooperative antipredator responses that characterise meerkat foraging groups (Hollén and Manser 2006). In both species, individuals above the age of independence were equally likely to survive, suggesting that the different antipredator and foraging strategies displayed by yellow mongooses and meerkats are similar in the efficiency of predation avoidance.

Yellow mongooses' and meerkats' distinct foraging group sizes appear to reflect very different optimal foraging

group sizes for these species, constrained by more than just prey choice. Meerkats tend to forage in sizeable groups and may not be able to resort to low-cost vigilance strategies in small groups, which have a high risk of dying out due to predation (Clutton-Brock et al. 1999a). In contrast, yellow mongooses' increased wariness in foraging groups appears to detract from their foraging success—even where their diet is almost exclusively invertebrate—and may thus preclude the permanent formation of larger foraging groups. Meerkats, in the social clade of herpestids, and yellow mongooses, in the solitary clade, have evolved separately since the early Pleistocene (Veron et al. 2004; Perez et al. 2006). Over time, species-specific foraging group sizes appear to have coevolved or led to highly distinct vigilance patterns, both strategies resulting in similar sustainable survival rates. We propose that even in areas where vertebrates are not a usual component of yellow mongoose diets, a switch from a solitary to potentially beneficial social foraging strategy would require a complex set of changes in antipredator behaviour. In herpestids, not only habitat and prey preference but also distinct vigilance patterns impose constraints on foraging group size, thereby affecting the potential development of social foraging.

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