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DIPLOMARBEIT

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Benefits of secondary predator cue inspection and recruitment in a cooperative mammal (*Suricata suricatta*)

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Acknowledgements

Zusammenfassung

Raubdruck und die Gefahr gefressen zu werden ist ein entscheidender Faktor im Leben beinahe jeden Tieres. Aus diesem Grund ist es nicht weiter verwunderlich, dass potentielle Beutetiere zahlreiche Anpassungen zur Vermeidung dieser Gefahr zeigen. Indirekte Hinweise auf die Anwesenheit von Raubfeinden als Indikator für die unmittelbare Bedrohung an einem bestimmten Ort und zu einer bestimmten Zeit zu beachten ist eine Möglichkeit zur Verringerung des Risikos. Bei vielen Säugetierarten konnte gezeigt werden, dass Individuen auf den Geruch von Prädatoren reagieren. Indirekte Hinweise können aber auch visuell oder akustisch wahrgenommen werden. Häufig erhöhen Tiere ihre Wachsamkeit, suchen vermehrt Schutz auf oder beenden die Futtersuche in betroffenen Gebieten. Folglich nehmen sie weniger Nahrung auf. Man kann aber davon ausgehen, dass Tiere durch diese Anpassungen die Gefahr verringern, selbst zur Beute zu werden.

Bei kooperativ organisierten Tierarten kann ein Individuum, welches Hinweise auf Beutegreifer erkennt, nicht nur selbst schneller reagieren, sondern auch zusätzlich profitieren, wenn es seine Gruppenmitglieder über die Gefahr informiert. Wenn jedes Individuum der gewarnten Gruppe Verhaltensweisen zur Feindvermeidung verstärkt, nützen diese Maßnahmen allen Mitgliedern. Verglichen mit einer Situation ohne Informationstransfer, ermöglicht die geteilte Wachsamkeit unter Umständen dem Individuum, welches den indirekten Hinweis findet, mehr Zeit für andere Aktivitäten, wie beispielsweise Nahrungssuche, verwenden zu können.

Erdmännchen (*Suricata suricatta*) sind eine hochsoziale Mangustenart, die im südlichen Afrika vorkommt. In der spärlichen Vegetation der Halbwüste finden sie wenig Deckung und sind einem hohen Raubdruck ausgesetzt. Sie haben ein sehr effizientes Wachsystem entwickelt und reagieren stark auf jeden Stimulus, der auf Raubfeinde hinweist. Ein Erdmännchen, das einen solchen Hinweis wahrnimmt, ruft mittels spezieller Rekrutierlaute seine gesamte Gruppe zusammen. Alle Mitglieder unterbrechen die Nahrungssuche und inspizieren den Stimulus. Wenn kein Räuber entdeckt wird dauert die Inspektion einige Minuten. Anschließend beginnen die Erdmännchen wieder mit der Nahrungssuche. Durch diese Informationsmöglichkeit kann sich jedes Gruppenmitglied auf die mögliche Gefahr einstellen und seine Wachsamkeit erhöhen, was wiederum der gesamten Gruppe zugute kommt.

In dieser Arbeit wurde ein experimenteller Ansatz gewählt um bei frei lebenden, an Menschen habituierten Erdmännchen, drei Hypothesen zu testen:

1) Erdmännchen entdecken einen Raubfeind früher, nachdem sie mit einem indirekten Hinweis auf den Räuber, wie z.B. dem Geruch konfrontiert worden sind.

2) Wenn kein Räuber entdeckt wird, aber alle Tiere in der Gruppe zu dem indirekten Hinweis rekrutiert werden, verbringt jedes Individuum während der folgenden Nahrungssuche mehr Zeit mit Verhaltensweisen zur Feindvermeidung.

3) Wird durch experimentelle Manipulation die Kommunikationsmöglichkeit unterbunden, so bleibt jenes Individuum, das den indirekten Hinweis findet, das Einzige in der Gruppe, das über die erhöhte Gefahr Bescheid weiß. Folglich muss dieses Individuum seine Futtersuche im Vergleich zur Normalsituation, in der es seine Gruppenmitglieder rekrutiert verringern.

Um diese drei Hypothesen zu testen wurden zwei unterschiedliche Experimente durchgeführt. In beiden Experimenten kamen indirekte Hinweise auf Raubfeinde wie Katzenurin, Katzenhaar (*Felis Catus*) Löffelohrenhundfell (*Otocyon megalotis*), oder Wüstenluchsfell (*Caracal caracal*) zur Anwendung. Im ersten Versuch wurde die Zeit gestoppt, welche die Erdmännchen benötigten, mit und ohne indirekten Hinweis einen Raubfeind zu entdecken. Im Zweiten hingegen wurde ein Hinweis ohne Anwesenheit eines Raubfeindes präsentiert und zu Vergleichszwecken das Rekrutieren möglich oder unmöglich gemacht.

Die Ergebnisse zeigten, dass Erdmännchen tatsächlich früher auf eine Räuberattrappe in Form eines ausgestopften und präparierten Karakals reagierten, wenn sie vorher einen indirekten Hinweis in Form von Geruchsspuren fanden. Damit konnte erstmals experimentell nachgewiesen werden, dass Tiere die Möglichkeit haben Räuber früher zu entdecken, wenn sie auf indirekte Hinweise wie Geruchsspuren treffen. Dies legt nahe, dass die Reaktion auf potentielle Gefahr in Form eines Hinweises auf die Präsenz eines Räubers die Überlebenswahrscheinlichkeit für Beutetiere erhöht.

Wenn allerdings, wie im zweiten Experiment, kein Räuber zu sehen war begannen die Erdmännchen wieder mit der Nahrungssuche. So reduzierten alle Tiere die für Nahrungssuche aufgewendete Zeit zugunsten von Verhaltensweisen zur Räubervermeidung. Dieser Effekt ist ähnlich stark ausgeprägt in Tieren, die rekrutiert wurden und in Tieren die rekrutierten.

Wurde hingegen der Rekrutierruf des mit dem Räuberstimulus konfrontierten Individuums durch gleichzeitiges Abspielen eines Playbacks mit weißem Rauschen im gleichen Frequenzbereich gestört, zeigte die Gruppe keine Reaktion auf den Rufer. Die Gruppe konnte dann den Räubergeruch auch nicht wahrnehmen. Wurde nun die Zeit, die das rekrutierende Tier nach einer erfolgreichen und nach einer durch Manipulation erfolglosen Rekrutierung in Feindvermeidung investierte verglichen, zeigte

sich kein signifikanter Unterschied. Allerdings hielt sich das Tier bei der verhinderten Rekrutierung häufiger an geschützten Plätzen auf, als wenn es die Gruppe informieren konnte.

Diese Ergebnisse deuten darauf hin, dass Erdmännchen als Reaktion auf die experimentell unterbundene Kommunikation möglicherweise Einbußen in der Effizienz der Futtersuche erleiden, da sie sich vermehrt in Deckung aufhalten. Daraus lässt sich schließen, dass der Hauptvorteil für das Erdmännchen, welches den Hinweis findet, darin besteht, dass ein Räuber entweder während der Inspektion des Hinweises durch die gesamte Gruppe oder während der anschließenden Futtersuche früher entdeckt wird. Diese frühe Entdeckung erhöht die Überlebenswahrscheinlichkeit für alle Gruppenmitglieder, was wiederum Vorteile mit sich bringt, wenn es darum geht das Revier zu verteidigen oder andere Raubfeinde zu entdecken („viele Augen sehen mehr als wenige"). Daher ist die Reaktion auf indirekte Raubfeindhinweise wie Geruchsspuren vorteilhaft, auch wenn sich kurzfristig die Zeit für Nahrungssuche für alle Erdmännchen einer Gruppe verringert. Schlussendlich legen die Ergebnisse nahe, dass das rekrutierende Individuum von der frühen Entdeckung des Räubers so stark profitiert, dass sich das Rekrutieren auszahlt, obwohl sich dadurch die Dauer der Nahrungssuche für diese Tier nicht erhöht.

Secondary predator cues enable meerkats to detect a predator earlier

Abstract

The responses of animals to olfactory, visual or acoustic secondary predator cues are manifold. Behavioural responses probably help to detect the potential predator earlier. We tested this assumption by presenting a full-mounted caracal (Caracal caracal) to wild meerkats (*Suricata suricatta*) in their natural habitat while simultaneously confronting the animals with either an olfactory secondary predator cue or a control cue. The caracal was detected earlier by the meerkats when a secondary predator cue indicating the presence of a terrestrial predator was presented. This is the first experimental evidence that exposure to a secondary predator cue enables animals to detect a predator earlier. We suggest that early detection increases prey survival chances and therefore even costly behavioural adaptations result in a fitness advantage.

Introduction

Virtually all animals face a major trade-off between the risk of starvation and predator avoidance (Brown and Kotler 2004; Lima and Dill 1990; Verdolin 2006). Therefore, it is highly beneficial for individuals to assess the actual predation risk and adjust their anti-predator investment according to the perceived danger. Evidence for this adjustment has been demonstrated in a number of species (Barta et al. 2004; Benhaiem et al. 2008; Daly et al. 1992; Jordan et al. 1997; Lima and Dill 1990; Sweitzer and Berger 1992).

Secondary predator cues are indicators of nearby predators and present an opportunity to assess the current level of danger. These indicators can be perceived in different sensory modalities. In mammals, however, olfactory perception is crucial (Apfelbach et al. 2005). Mammals have been shown to respond to predator odours with changes in spatial activity, feeding rate, increased vigilance and other behavioural changes (Apfelbach et al. 2005; Berger et al. 2001; Shrader et al. 2008; Sündermann et al. 2008). Moreover, several theoretical models assume that short-term changes in foraging behaviour minimise predator exposure and encounter rate (Lima and Dill 1990; Lima et al. 1998), thereby increasing survival rates for prey species. Experiments have demonstrated that vigilant animals spot predators at larger distances than foraging ones (Lima and Bednekoff 1999a); such vigilant animals are probably less vulnerable to predation (Fitzgibbon 1989). However, we lack experimental evidence that the various reactions to predator odours enable animals to detect predators earlier and likely increase survival.

One important model for behavioural decision-making is "the predation risk allocation hypothesis" (Lima and Bednekoff 1999b). It predicts that animals interrupt foraging during short periods of high risk, before they resume feeding under less risky circumstances. The common expectation is that animals will discover a predator earlier during such periods of interrupted foraging. The assumption that the reaction to predator cues is adaptive and increases the chance for prey species to detect a predator earlier has never been tested experimentally.

Meerkats (*Suricata suricatta*) are small carnivores living in cooperative breeding groups in southern Africa. They face high predation pressure by aerial and terrestrial predators and have developed a coordinated sentinel system (Clutton-Brock et al. 1999b) involving an elaborate spectrum of alarm calls encoding referential as well as motivational information (Manser et al. 2002). When a meerkat encounters a secondary predator cue such as cat urine, cat hair, fox hair, caracal fur (originating from *Felis catus*, *Otocyon megalotis*, *Caracal caracal*, respectively) or different kinds of predator faeces, it reacts immediately by emitting recruitment calls (Manser 2001) causing the group to interrupt foraging and approach the calling individual in order to inspect the cue (Manser et al. 2001).

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We conducted an experiment to test whether, in wild meerkats, the presentation of a secondary predator cue leads to an earlier response to a predator. Our prediction was that predator detection would be faster under exposure to a secondary predator cue versus a control cue.

Material and Methods

The study animals

The experiments were performed with wild meerkats in and around the Kuruman River Reserve in South Africa, between June and August 2008. The study site is located 30 km west of Van Zylsrus, in the southern part of the Kalahari desert (Clutton-Brock et al. 1999a). The seven groups used in the experiment were habituated to human presence (closer than 0.5m) and consisted of adult, sub adult and juvenile meerkats (older than one year, six to twelve months and three to six months, respectively). During the study period, no pups were present in the experimental groups (younger than three months). The median group size was eleven individuals (range 6 to 17). All groups were part of the long-term study population of the Kalahari Meerkat Project (Clutton-Brock et al. 1999a). Individual recognition is provided by unique dye marks and, usually, one individual per group is equipped with a radio collar.

Secondary predator cues (SPC)

As secondary predator cues we used derivates from sympatric terrestrial predators that had previously been shown to elicit a response by meerkats (Graw and Manser 2007; Lienert 2007; Manser 2001). We used domestic cat hair, domestic cat urine and bat-eared fox fur. The cat hair was obtained from a local domestic cat, the bat-eared fox fur originated from road kills (not older than 24 h), and the cat urine from a local veterinarian. The derivates were stored at -20 °C and defrosted shortly before they were used in the experiment. Whereas the bat-eared fox fur was used alone, the cat hair was combined with cat urine for the presentation. This yielded two different kinds of experimental cues, the fox cue and the cat cue. Although these two kinds represent different terrestrial predators, the meerkats responded with the same kind of recruitment calls (high urgency calls (see Manser 2001 for definition)) in all experimental exposures. Moreover, several documented encounters with wildcats and bat-eared foxes triggered anti-predator responses by the meerkats (Graw and Manser 2007). As a control cue we used antelope hair treated in the same manner as the secondary predator cues. The antelope hair was obtained from animals killed during routine hunting for meat.

The caracal detection experiment

Each meerkat group was tested twice. In the experimental treatment we placed a secondary predator cue in the centre of the group. As soon as one of the group members inspected the cue and emitted the first recruitment call, we started to move a full-mounted caracal parallel to the group in an average distance of 78.3 m (range: 49 to 142 m). The calls were usually given immediately when the

meerkat sniffed at the cue (Zöttl, pers. observation). The dummy predator was fixed on a sledge with wheels and a 20 m string. Until we started to move it, the mounted caracal was hidden behind a camouflage fabric and was therefore invisible for the group. We measured the latency of predator detection defined as the time from the first recruitment call (released in response to the secondary predator cue) until the first terrestrial alarm call in the group (in response to the mounted caracal). In the control treatment, we placed a control cue in the centre of the group and started moving the caracal; we then measured the latency when the first meerkat had inspected the control cue. According to our assessment this is the point which corresponds optimally to the time of the first recruitment call in the experimental treatment. Since no recruitment calls were given to the control cue, the group showed no response to the presentation.

Before and after the experiment the meerkats showed no reaction to the experimental equipment (camouflage cloth, the caracal under or behind the fabric, or the person pulling the caracal; Zöttl, pers. observation). To control for order effects, half of the experimental groups started with the experimental treatment, whereas the other half started with the control treatment.

We attempted to standardize the distance between the group and the caracal in the experimental and control treatments. Since this was often not possible due to vegetation, we chose a larger distance in the experimental than in the control treatment. This excludes the proximity to the predator as an alternative explanation for faster predator detection (Table 1). We did not control for effects of wind directions because we assumed that a several-years-old, mounted cat fur would not exude any relevant odours and because meerkats have shown a diminished response to old predator odours even after one day (Lienert 2007). The distance from the group centre to the location where the caracal was detected by the meerkats was measured with a rangefinder (Leica). To avoid effects of habitat structure, we performed both treatments in one group in the same landscape and vegetation, differentiating between sand dunes, hilly areas, as well as flats with bushes and flats without bushes. We tried to avoid differences in the visibility of the predator due to vegetation, but if this was impossible, we accepted the predator to be less visible in the experimental treatment. To control for visibility subsequent to the experiment, we took a photograph from the presentation spot towards the caracal. The camera was positioned at a standard height of 35cm, which is equivalent to the head position of a guarding meerkat on the ground. Later, these photos where shown to 12 naïve human observers, who were asked to score the visibility of the predator on a three-stage scale (good, medium, poor). The modal values were calculated for each presentation (Table 1). We also ensured that, at the time of the presentation, there were no meerkats in a raised guard position (look-out position at least 10 cm above ground) or meerkats emitting sentinel calls (Manser 1999). Finally, we only performed an experiment when at least 80% of the group were engaged in foraging activity.

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Table 1. Experimental conditions for the experimental (SPC) and control treatment in each meerkat group. Visibility, distance to the predator and landscape are displayed.

	Visibility		Distance to the predator (m)		Landscape	
Group	SPC	Control	SPC	Control	SPC	Control
KU	good	good	142	87	Dunes	Dunes
F	good	good	51	49	Flats without bushes	Flats without bushes
D	medium	medium	94	95	Flats without bushes	Flats without bushes
AZ	poor	medium	93	78	Flats with bushes	Flats with bushes
W	poor	medium	80	64	Flats with bushes	Flats without bushes
L	poor	medium	90	56	Hilly	Hilly
CD	poor	poor	64	53	Flats with bushes	Flats with bushes

Statistical analyses

All analyses were calculated using non-parametric tests (SPSS 15.0).

Results

The latency to the first terrestrial alarm call in response to the presented full-mounted caracal was significantly shorter when the meerkat groups were exposed to a secondary predator cue compared to a control cue (Wilcoxon; Z=-2.4; p=0.018; N=7; Figure 1).
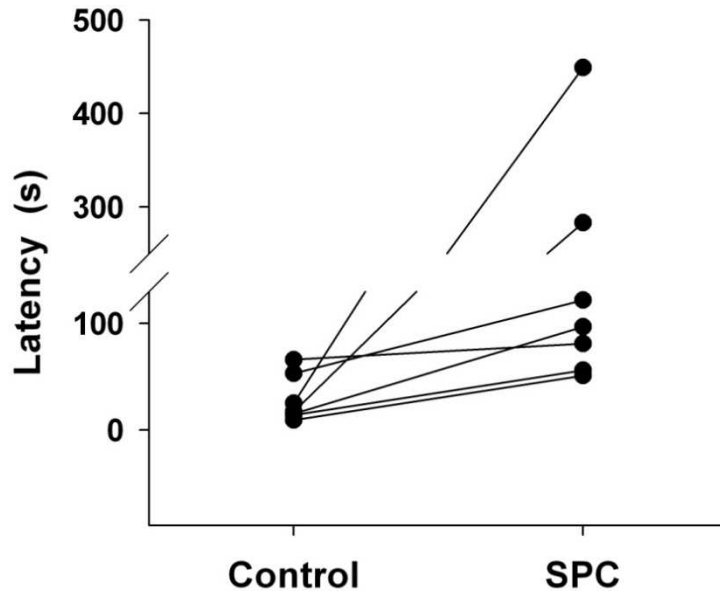
Figure 1. Latency to the first alarm call given to the dummy predator of meerkat groups (n=7) in the control treatment and in the experimental treatment (SPC)

Discussion

When detecting a secondary predator cue, the meerkat that encountered the cue started emitting recruitment calls, causing the rest of the group to interrupt foraging and all group members to

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approach and inspect the cue (Manser 2001; Manser et al. 2001). This behaviour is costly because the meerkats lose foraging time and thus food intake decreases. Our results, however, show that meerkats are able to detect a predator earlier when exposed to a secondary predator cue indicating the presence of a terrestrial predator. The latency to the first alarm call was significantly shorter when the meerkats encountered a secondary predator cue compared to a control cue.

That early predator detection is a crucial parameter predicting prey survival has been assumed frequently in theoretical work (Bednekoff and Lima 1998; Pulliam et al. 1982). Nonetheless, there is scarce evidence that high rates of vigilance are not always related to predator detection (Baldellou and Peter Henzi 1992). A broad body of literature documents behavioural changes as response to predator odours (reviewed in Apfelbach et al. 2005; Stoddart 1980), and numerous authors assume explicitly or implicitly that animals increase their survival rates by reacting to secondary predator cues (Berger et al. 2001; Boag and Mlotkiewicz 1994; Borowski 2002; Dell'omo and Alleva 1994; Dickman 1992; Endres et al. 2005; Ferrari et al. 2006; Laska et al. 2005; Lienert 2007; Lohrey et al. 2009; Monclús et al. 2005; Roth Ii et al. 2008; Ward et al. 1997). However, this has never been tested experimentally. Our study provides the first experimental evidence supporting this assumption.

Presumably, benefits of early predator detection outweigh the costs of decreased food intake, resulting in the persistence of the response to secondary predator cues. Nevertheless, other benefits from secondary predator cue inspection and recruitment of group members to the cue are conceivable and have not been quantified in our experiment. The fact that recruiting group members ensures information transfer and as a consequence every individual is aware of the magnified predation risk allows the costs of anti-predator behaviour to be shared among group members, which potentially benefits all group members, but in particular the individual recruiting others (Zöttl et al. unpublished data). These benefits would become especially important in a foraging session subsequent to a secondary predator cue encounter when no predator has been detected by the group.

Interestingly, the individual that recruited the group was not always the first to give the alarm call in response to the dummy predator, suggesting that individuals benefits from recruitment rather than from the secondary predator cue encounter per se. Unfortunately, the identity of the individual that spotted the predator first could not always be determined, making the sample size too small for statistical analyses. Note also that it was rarely the individual closest to the predator that gave the initial alarm call.

The risk allocation hypothesis predicts that animals stop foraging during infrequent periods of high danger (Lima and Bednekoff 1999b). By showing that meerkats do indeed interrupt foraging and are more likely to spot a predator during this interruption, we present indirect support for the risk allocation hypothesis. Experiments manipulating the frequency and the extent of perceived danger would be the next step in testing this hypothesis. Meerkats provide an ideal system to test this

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hypothesis because they adjust their behaviour to cue freshness (Lienert 2007) and apparently encode risk dependence (Manser, unpub. data). This would allow to control if the manipulation of the perceived danger succeeded.

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Costs and benefits of communication about secondary predator cues in meerkats

Abstract

In socially foraging species the exchange of information on perceived predation risk among group members enables each individual to adjust anti-predator behaviour to the immediate level of danger. One way of adjustment is to attend to secondary predator cues. In cooperatively breeding meerkats (*Suricata suricatta*), which forage in social units and display coordinated anti-predator behaviour, individuals encountering a secondary predator cue respond immediately by recruiting the group. We investigated experimentally the benefits and costs of this behaviour for the actor (recruiter) and the recipients (recruited group members) in wild meerkats. Presentations of secondary predator cues caused the group to interrupt foraging and to inspect the cue. In subsequent foraging sessions, meerkats increased their anti-predator behaviour and decreased the time spent foraging. When the actor was confronted with a secondary predator cue but recruitment was disabled by a playback of white noise in the same frequencies as the recruitment call, the group continued foraging as expected and did not inspect the cue. Interestingly, the actor did not change its anti-predator or foraging behaviour regardless whether recruitment was experimentally disabled or not. Nevertheless, it spent more time in sheltered locations when recruitment had been impeded. We therefore argue that the major selective force behind recruitment as a response to secondary predator cues is early predator detection by any group member due to increased anti-predator behaviour of all individuals.

Introduction

The risk of being injured or killed by a predator can have immediate and severe consequences on an individual's fitness, whereas decreased foraging activity or mating possibilities may have less influence on lifetime fitness (Lima and Dill 1990). Thus, the impact of predation on animal behaviour and decision making is expressed in a broad range of behavioural adaptations. These include increased vigilance (Berger et al. 2001; Sweitzer and Berger 1992; Winnie Jr and Creel 2007), reduced exposure by cover seeking (Kats et al. 1988) or by minimized activity (Holomuzki and Short 1990; Orpwood et al. 2008), adaptations in habitat choice (Jordan et al. 1997) and also adjustments in reproductive strategies (Fontaine and Martin 2006). Some of these anti-predator behaviours are mutually exclusive to fitness-related activities like foraging (e.g. being vigilant). Others, like altering movement patterns or differences in habitat choice to avoid predation, can incur costs due to the exploitation of safe but less profitable foraging patches (Powell and Banks 2004). According to the marginal value theorem, animals should abandon a foraging spot when the return rate no longer exceeds the foraging costs (Charnov 1976). Nevertheless, predation pressure can force foraging animals to change to a safer foraging patch much earlier than predicted by the theorem (Brown 1988, 1992; Lima 1998). Consequently, foraging animals face a trade-off between maximizing energy, which reduces the risk of starvation, and minimizing the risk of being preyed upon, which increases survival (Lima and Dill 1990; Verdolin 2006).

Due to ubiquitous variations in predation pressure over time and space, the optimal decision on how much to invest into foraging effort versus anti-predator behaviour depends on the actual level of danger at the specific time and place. That animals are able to identify fluctuations in the danger of being predated has been shown repeatedly (Benhaiem et al. 2008; Lima and Dill 1990; Verdolin 2006). One way of assessing the current level of danger is by attending to secondary predator cues, which are indicators of predator presence. In mammals, predator odours are crucial (Apfelbach et al. 2005) and certain anti-predator responses shown to increased predation pressure in general are also found in this special odour context, like reduced foraging effort (Ward et al. 1997), increased vigilance (Berger et al. 2001; Monclús et al. 2005) and different utilization of landscape (Apfelbach et al. 2005; Shrader et al. 2008).

Since the "information centre hypothesis" was forwarded (Ward and Zahavi 1973), information transfer in animal aggregations has received increasing attention. Originally suggested for foraging opportunities, the social acquisition of information in a variety of contexts is now widely accepted. Abundant empirical evidence supports the importance of social information in foraging decisions, habitat selection and mate choice (reviewed in Danchin et al. 2004). However, apart from field studies of alarm calling behaviour (Blumstein 1995; Dunford 1977; Manser 2001; Marler 1957; McGowan and Woolfenden 1989; Seyfarth et al. 1980; Smith 1992), only little attention has been paid to communication about the perceived level of danger. In particular in those species that display a

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coordinated vigilance system and anti-predator behaviour, individuals potentially benefit from communicating personally acquired information. Communication about immediate danger theoretically offers multiple benefits to both the individual that sends a signal (actor) and the individuals affected by the actor's behaviour (recipients) (terminology based on West et al. 2007).

Meerkats (*Suricata suricatta*), cooperatively breeding mongooses, provide a unique model system to gain insights into the costs and benefits arising through communication of perceived predation risk via secondary predator cues. These small carnivores live, breed and forage in social groups of up to 50 individuals in Southern Africa (Clutton-Brock et al. 2005). Meerkats are particularly vulnerable to predation when digging for prey because their view is limited during extractive foraging techniques (Clutton-Brock et al. 1999b). Moreover, they forage in open habitats and face a high predation pressure by aerial and terrestrial predators. As a result they have evolved a coordinated sentinel system (Clutton-Brock et al. 1999b) and employ an elaborate spectrum of alarm calls encoding referential as well as motivational information (Manser et al. 2002).

Meerkats respond strongly to olfactory secondary predator cues. An individual that encounters a secondary predator cue, e.g. cat urine, immediately emits recruitment calls (Manser 2001) that cause the group to interrupt foraging and approach the calling individual (Manser et al. 2001). Individuals start giving recruitment calls when approaching and inspecting the cue (Manser et al. 2001). During this group inspection, individuals scan the surroundings for predators; they detect predators faster due to secondary predator cue encounters (Zöttl et al. Unpublished data). If no predator is detected the group resumes foraging after several minutes. Hence, by recruiting its group members the meerkat that encountered the cue first transfers its personal information about the increased level of danger to the group. This makes each individual aware of the increased risk. If meerkats increased their anti-predator behaviour during the subsequent foraging session, the actor (who initially encountered the cue) gains the benefit of increased anti-predator behaviour by the other group members. Successful recruitment may therefore allow the individual that initially encountered the cue to invest more time in foraging compared to a situation in which it is unable to inform the group members. In addition to early predator detection by any group member (Zöttl et al. Unpublished data), the benefit of reduced costs for the actor due to information transfer may be one incentive for persistence of recruitment behaviour.

In this study, on wild meerkats we used an experimental approach to test two hypotheses:

1) The presentation of a secondary predator cue increases the anti-predator behaviour of the actor and the recipients in a subsequent foraging session, if recruitment occurs and the group can inspect the cue.

2) The actor shows a higher increase in its anti-predator behaviour if the intended recruitment is experimentally disabled and its group members therefore remain naïve to the actor's perceived enhanced predation risk.

Material and Methods

The study animals

The study was conducted with wild meerkats (*Suricata suricatta*) at the Kuruman River Reserve (26°58'S, 21°49'E). A detailed ecological description is provided in Clutton-Brock et al. (1999a). Between April and August 2008 we worked on eight meerkat groups, resulting in a total number of around 80 individuals. All groups were part of the long-term study population of the Kalahari Meerkat Project (Clutton-Brock et al. 1998). Individual recognition was provided by unique dye-marks, and all animals were habituated to close human observation (<1 m), allowing experimental manipulation. In each group, one of the meerkats had a radio collared fitted.

The experimental set-up

The experiment consisted of three treatments, namely the "SPC (secondary predator clue) public", the "SPC private" and the "control" treatment (for description see below). In this experiment we randomly assigned one adult individual to be the actor (the individual confronted with the predator or control cue and that did or did not recruit the group) and another one to be the potential recipient (West et al. 2007). The selected recipient represented any group member that, depending on the treatment, was recruited or not recruited to inspect the cue. The individuals remained the same in all three treatments. The experiments were started at the earliest 30 min after the researchers encountered a group, ensuring that the group was foraging normally. This initial phase was followed by a 10-min observation period (hereafter referred to as "before cue presentation"). Subsequently, we prepared the secondary predator cue presentation, presented the cue and conducted a second 10-min observation period (hereafter "after cue presentation").

The experimental secondary predator cue and the control cue

As secondary predator cues we used derivates from sympatric, terrestrial predators known to elicit a recruitment response by meerkats (Graw and Manser 2007; Lienert 2007; Manser 2001). Specifically, we used domestic cat hair, domestic cat urine, fox fur and caracal fur, originating from

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domestic cats (*Felis catus),* bat-eared foxes *(Otocyon megalotis)* and caracals *(Caracal caracal).* To ensure matched samples between the treatments, we used the same kind of secondary predator cue in all treatments of a particular trial. Usually cat hair and caracal fur were combined with cat urine as the experimental secondary predator cue (12 out of 19 cases). However, some cues were also used alone (bat-eared fox fur (2), caracal fur (1), cat hair (3) and cat urine (1)). Logistic considerations under field conditions prevented the use of a standardised cue. Moreover, meerkats show rapid habituation to false alarm calls (Schibler and Manser 2007): using several different cues therefore helped reduce the risk of habituation to experimental secondary predator cues .

The cat hair was obtained from a local cat, the bat-eared fox fur originated from road kills, the caracal fur from the local taxidermist and the cat urine from a local veterinarian. All derivates, except the caracal fur, were immediately frozen after they were obtained, stored at -20 °C and defrosted shortly before use. The caracal fur was stored in salt for three days and kept frozen afterwards by the taxidermist. No cue was used twice in an experiment.

As a control cue we used antelope hair, squirrel hair (*Xerus inauris)*, human hair or human urine treated in the same way as the secondary predator cue. The antelope hair originated from Oryx antelopes (*Oryx gazelle*) that were hunted on a farm, the human hair and urine were obtained from different persons living in the Kuruman River Reserve. The squirrel fur was obtained from a road kill.

The cue presentation
The secondary predator cue was tied around a stone and connected with a transparent fishing line to a thin stick. A scorpion was fixed in the same manner to another stick and was used to catch the attention of the meerkat that was chosen to be the actor. Both scorpion and cue were kept in different airtight plastic boxes until used. As soon as the actor saw the scorpion he moved several meters (range 3 to 10 m) away from the group. We allowed the actor to grasp the scorpion and waited until it began feeding.

"SPC public" treatment: The secondary predator cue was placed close to the actor. As soon as it noticed the cue, it started recruiting the group. All group members interrupted foraging and started to inspect the cue. After the group had finished the cue inspection and as soon as 80% of the group members resumed foraging, a second 10-min observation period started.

"SPC Private" treatment: the presentation was done as above, but at the point when the actor started to inspect the cue, white noise was played back. It covered exactly the frequencies meerkats use in recruitments calls. Previous to the experiments the meerkats were habituated to the white-noise playback. Here, the playback prevented call perception by the group and the meerkats kept on foraging. As soon as the actor started to forage again, the second observation period was started. The individual chosen as the recipient in this treatment was naive to the actor's secondary predator cue

encounter because it neither perceived the recruitment calls (due to the playback) nor inspected the predator cue. Our method of disabling recruitment was successful because otherwise the group would have responded to the recruitment calls. In order to control for other playback effects, a 30-sec control playback was performed previous to each 10-min observation period in all treatments.

Control treatment: We presented a control cue which was prepared like the secondary predator cue to the actor. The presentation procedure remained unchanged and the second 10-min observation period of both the actor and the recipient was started as soon as the actor resumed foraging. Like in the SPC private treatment, the recipient had not been recruited (usually no recruitment calls were emitted) and was therefore assumed to reflect unmanipulated foraging activity.

Behavioural observations

To compare foraging behaviour prior to and after cue presentations, we employed two different sampling methods, focal animal and scan sampling, simultaneously (following Martin and Bateson 2007). Two observers simultaneously performed a 10-min continuous focal animal sampling session, one on the actor and one on the recipient. The observers followed the focus individuals in a 1 - 2 m distance, filming the animals with two digital video cameras (JVC Everio Camcorder, Sony Digital Camcorder).

The scan sampling protocol was used to record the guarding behaviour of all individuals in the group, and to document the spatial cohesion of the focal individual and the other group members as well as the movement of actor and receiver. In a 10-min sampling interval we recorded how many individuals were in guarding position, defined as either in an upright position on two legs on the ground (guarding see appendix) or on elevated positions (raised guarding see appendix). Moreover, we recorded the distances of actor and recipient to the closest adult individual (as a measure of how wide the group was spread out) in a two-minute interval, as well the distance the actor and recipient moved during the last sample interval.

Naturally occurring alarm calls and predator encounters during the observation period

In case of predator alarms and resulting foraging stops of the group during the observation period before the cue presentation, we interrupted recording until 80% of the group was foraging again. If the group interrupted foraging for more than 4 minutes we cancelled the observation period completely and started a new 10-min observation period after the group resumed normal foraging activity. Since we needed the first 10 min of post-cue foraging to ensure matching samples between the treatments, we accepted short foraging interruptions due to naturally occurring alarm calls after the cue presentation. However, if at least 80% percent of the group interrupted foraging for more than 4 minutes, the experiment was cancelled completely and repeated earliest a week later. The total number of alarm calls during the 10-min observation periods after the cue presentations did not differ between

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the three treatments (Friedman; N=19, Chi²=1.66, p=0.44; Mean Rank: 1.82, 2.05, 2.13 for control, SPC private and SPC public, respectively) and are therefore unlikely to have induced significant differences in behaviour.

Video analyses and data processing

The videos taken during 10 min observation periods were saved as avi- or mod-files. For behavioural analyses we used the Observer XT program, whereby we measured the different parameters on a predefined ethogram (see appendix). For state behaviours, we recorded beginning and ending, whereas events were scored without duration. The state behaviours comprised two categories. Behaviours within the same category were mutually exclusive, whereas different categories were scored parallel. As a result behaviours of each category summed up to 10 min. After the behavioural analyses, we calculated the total duration for state behaviours and the total number for event behaviours.

The first scored category was individual behaviours performed by the filmed individual (actor or recipient), including 23 different behaviours. After the analyses we created groups of behaviours by merging several different behaviours depending on their functionality: anti-predator behaviours, foraging behaviours or neutral behaviours, i.e. those that are independent from foraging or predation (e.g. social interactions) or that were not clearly assignable to either of the two first categories (e.g. eating vigilantly). These groups were then treated like single state behaviours and their total duration was used for analyses.

Foraging behaviour included three different behaviours, namely digging, searching for food/ scratching the surface and eating/handling prey (see appendix for definitions). We were interested in the relative contribution of the two different foraging behaviours (digging and searching food/ scratching surface) to the summed foraging time. We therefore divided digging by searching food/ scratching surface and labelled the variable "foraging ratio". Higher values of this variable indicate a relatively high contribution of digging to the overall foraging duration. One individual, however, never performed searching food/ scratching surface in one of the 10-min observation periods and only dug. Since a division by zero is not possible, we replaced the missing value with the highest other value displayed by any individual and added 0.1. This is statistically permissible because we used a Wilcoxon rank test to analyse differences: this test does not account for arithmetic divergence but differences in ranks. Consequently, this case was scored with the rank 1, which reflects the biological situation as well as possible.

Anti-predator behaviour consisted of seven different behaviours, namely raised guarding, guarding, scanning, lying vigilantly, bolt hole inspection, bolt hole renovation and being below ground. Vigilance behaviour was defined as behaviour that increases the chances to detect, localize or recognize a predator (Apfelbach et al. 2005); it included raised guarding, guarding and scanning.

If the animals were briefly out of sight (mostly due to camera handling) we categorized them as "being out of sight". The average total duration of "being out of sight" during a 10-min observation period was 2.8±0.46 sec and is therefore unlikely to influence our results. In case an animal was out of the camera's view but still visible for the observer (e.g. due to vegetation) the observer described the focal animal's behaviour and the video was analysed based on the audio protocol.

The second scored category of mutually exclusive behaviours described the micro-environment in which the animal stayed. We defined two different states, sheltered or unsheltered (see appendix for definitions), which depended on the place where the individual performed the specific individual behaviour.

The data from scan sampling was processed by calculating the means of all scans made during an observation unit and using this value for further analyses (Martin and Bateson 2007).

Statistical analyses

All statistical analyses were performed using SPSS 15.0. We used parametrical tests when data fulfilled the criteria for normal distribution according to the Kolmogorow-Smirnov test. If the distribution differed significantly from normal distribution, we either log-transformed it to fit it into normal distribution or we employed nonparametric tests.

Results

Foraging behaviour

Both the actor and the recipient decreased their total foraging duration after the secondary predator cue presentation in the SPC public treatment (Paired T-test, N=19; actor: T=3.173, p=0.005; recipient: T=3.496, p=0.003; Fig. 1). No significant change in foraging time was found in any of the focal animals in the control treatment (Paired T-test, N=19; actor: T=-0.767, p=0.453; recipient: T=1.455, p=0.163; Fig. 1). In the SPC private treatment, the foraging time of the cue-exposed actor was significantly reduced (Paired T-test, N=19, T= 3.534, p=0.002). However, the recipient (not exposed to the cue in this treatment) did not change its foraging time (Paired T-Test; N=19, T=1.360 p=0.227). A comparison of actor foraging decrease in the SPC public versus SPC private treatment revealed no significant difference (Wilcoxon, N=19, Z=0.181, p=0.856).
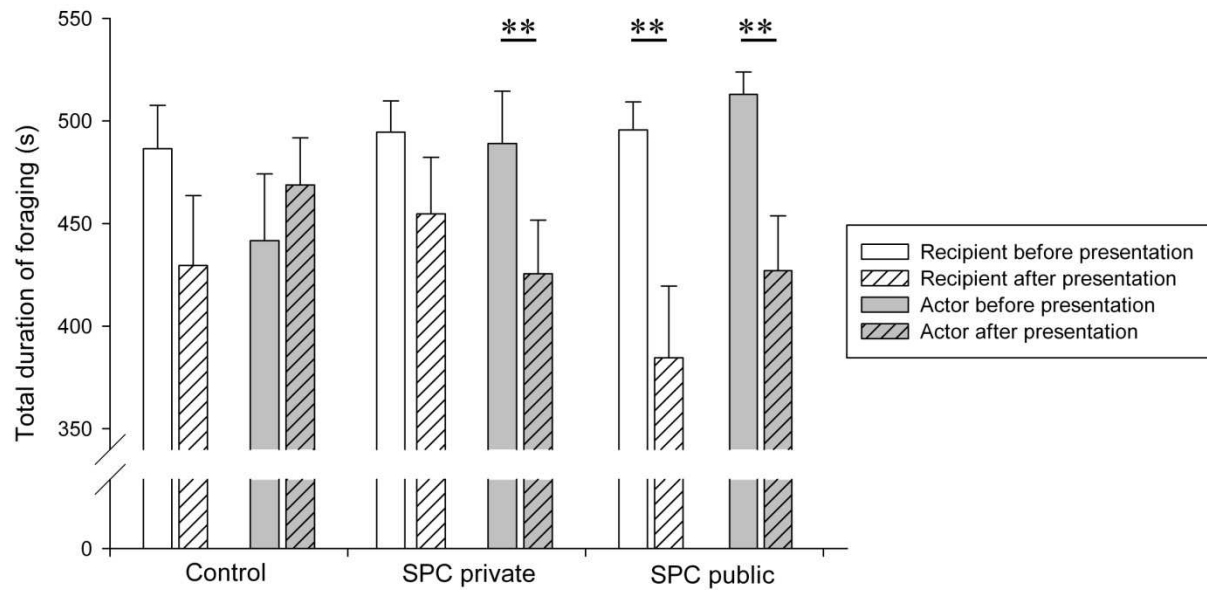
Figure 2. Comparison of the time spent foraging by actor and recipient during 10-min focal animal sampling in the control, SPC private and the SPC public treatment before and after cue presentation. Displayed is the mean + standard error (N=19). Double asterisks represent p-values < 0.01.

A more detailed examination of foraging behaviour showed that both searching food/scratching surface and digging behaviour, on their own, did not decline significantly (Tab. 1). Nevertheless, there is a trend toward reduced digging behaviour of the actor in the SPC public treatment. The relationships of searching food/scratching surface for actor and recipient in the SPC public treatment were insignificant (Tab. 1). When comparing the ratio of digging to searching food/ scratching surface in the different treatments, no difference was detected (Tab 1).

Anti-predator behaviour

Contrary to the foraging behaviour, the time investment into anti-predator behaviour increased for actor and recipient in the SPC public treatment after cue exposure (Paired T-Test, N=19; actor: T=-2.874, p=0.01; recipient: T=-2.976, p=0.008; Fig. 2). Similar to the results for foraging behaviour, anti-predator behaviour did not change significantly for either actor or recipient in the control treatment (Paired T-Test, N=19; actor: T=0.776, p=0.448; recipient: T=-1.656, p=0.115; Fig. 2). Like in the SPC public treatment, the actor increased the time invested in anti-predator behaviour in the SPC private treatment (Paired T-Test, N=19; T =-3.278, p=0.004), whereas the recipient did not (Paired T-Test, N=19; T=-0.879, p=0.391; Fig. 2). Paralleling the findings concerning foraging behaviour, the increase of anti-predator behaviour did not differ in the actor between SPC private and SPC public (Wilcoxon, N=19, Z=0.523, p=0.601).

Table 2. Different elements of foraging behaviour as well as their ratios. If a parametric test was applied, means are displayed for observations before and after cue presentations; medians are provided for non-parametrically tested data. For all tests, the sample size, the effect size and the p-value are displayed.

			Mean			T-Test	
			Before	After	N	Effect size (T)	P-value
Searching food/ scratching surface	Control	Recipient	358.11	331.84	19	0.74	0.47
		Actor	321.58	348.47	19	-1.13	0.28
	SPC private	Recipient	351.32	293.32	19	1.68	0.11
		Actor	293.32	282.95	19	0.30	0.76
	SPC public	Recipient	350.53	282.63	19	1.74	0.10
		Actor	362.37	324.32	19	1.63	0.12
Digging	Control	Recipient	117.53	95.21	19	1.36	0.19
		Actor	116.00	115.42	19	0.03	0.98
	SPC private	Recipient	138.53	156.84	19	-0.67	0.51
		Actor	185.79	140.89	19	1.39	0.18
	SPC public	Recipient	132.84	96.63	19	1.41	0.17
		Actor	142.42	97.42	19	1.78	0.09

|			Median			Wilcoxon test statistics	
			Before	After	N	Effect size (Z)	P-value
Ratio digging:searching food	Control	Recipient	0.26	0.25	19	0.28	0.78
		Actor	0.43	0.33	19	0.64	0.52
	SPC private	Recipient	0.36	0.44	19	0.97	0.33
		Actor	0.50	0.39	19	0.72	0.47
	SPC public	Recipient	0.33	0.32	19	0.04	0.97
		Actor	0.31	0.25	19	0.72	0.47

Vigilance behaviour

The recipient tended to scan less after the cue presentation in the control treatment, in contrast to the actor (no change; Tab. 2). Similarly to the actor in the control treatment, the individuals in the treatments SPC private and SPC public did not modify their time investment in scanning behaviour.

Table 3. Vigilance behaviour (log transformed) and different behaviours contributing to it. If a parametric test was applied, means are displayed for observations before and after cue presentations; medians are provided for non-parametrically tested data. For all tests, the sample size, the effect size and the p-value are displayed (if significant in bold) are displayed.

			Mean			Paired T-test	
			Before	After	N	Effect size	P-value
Vigilance	Control	Recipient	1.7	1.8	19	-0.50	0.25
		Actor	1.8	1.8	19	-0.18	0.77
	SPC private	Recipient	1.8	1.7	19	-0.08	0.49
		Actor	1.7	1.8	19	-1.37	0.43
	SPC public	Recipient	1.7	2.0	19	-2.29	**0.03**
		Actor	1.7	1.9	19	-2.42	**0.02**
			Median			Wilcoxon test statistics	
			Before	After	N	Effect size	P-value
Scanning	Control	Recipient	28	20	19	1.80	0.07
		Actor	22	20	19	0.85	0.39
	SPC private	Recipient	22	25	19	0.70	0.48
		Actor	18	31	19	1.26	0.21
	SPC public	Recipient	21	21	19	0.06	0.95
		Actor	24	29	19	0.10	0.92
Guarding	Control	Recipient	16	26	19	0.45	0.65
		Actor	23	32	19	0.38	0.70
	SPC private	Recipient	34	27	19	0.71	0.48
		Actor	21	22	19	0.81	0.42
	SPC public	Recipient	34	54	19	1.57	0.12
		Actor	24	61	19	2.25	**0.02**
Raised guarding	Control	Recipient	0	0	19	1.36	0.17
		Actor	0	0	19	0.40	0.69
	SPC private	Recipient	0	0	19	1.46	0.14
		Actor	0	0	19	0.37	0.72
	SPC public	Recipient	0	0	19	1.36	0.17
		Actor	0	0	19	0.00	1.00

Guarding was the only activity that differed significantly, after cue presentation, for the actor in the SPC public treatment (Tab. 2). In all other treatments and in the SPC public (recipient) no significant changes were detected (Tab. 2). None of the treatments revealed any significant change in raised guarding activity for actor or recipient (Tab. 2).
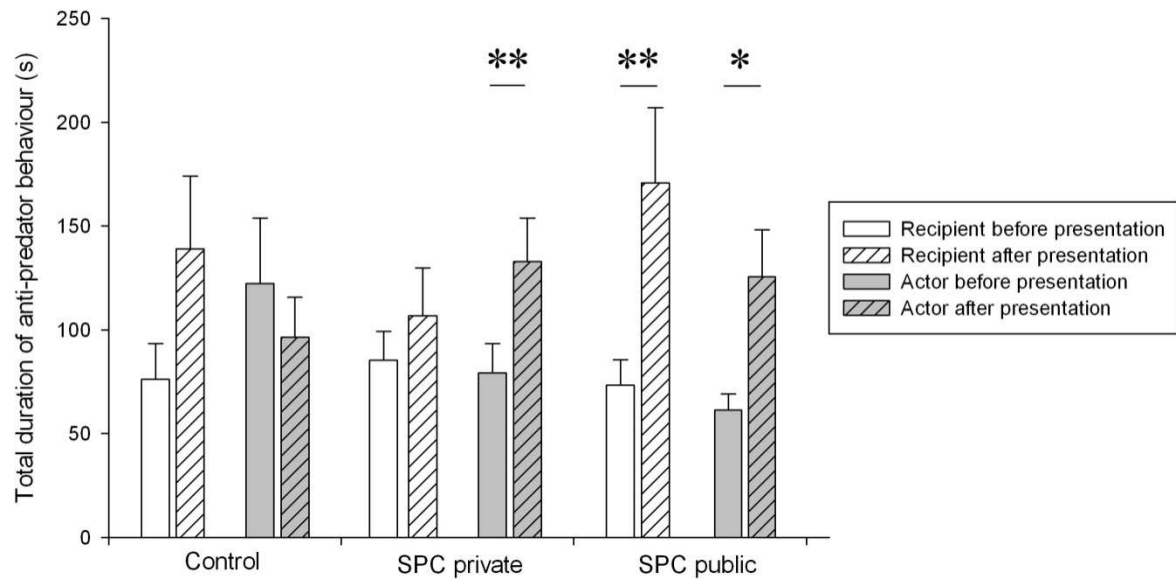
Figure 3. Time invested in anti-predator behaviour during 10-min observation periods in the control, SPC private and the SPC public treatment before and after cue presentation. Displayed is the mean + standard error (N=19). Double asterisks represent p<0.01 and single asterisks represent significance at a level of p<0,05.

Time spent in sheltered locations

The time spent in sheltered locations did not change for actor or recipient after cue encounter in the SPC public treatment (Wilcoxon, N=19; actor: Z=1.214 p=0.225; recipient: Z=-0.310, p=0.756; Fig. 3). Similarly, no change was detected in the control treatment (Wilcoxon, N=19; actor: Z=0.152, p=0.619; recipient: Z=0.497, p=0.879 Fig. 3). Interestingly, the actor increased the time spent in sheltered locations after cue presentation in the SPC private treatment (Wilcoxon, N=19; Z=2.864, p=0.004), whereas the recipient did not (Wilcoxon, N=19; Z=1.046, p=0.295, Fig. 3).
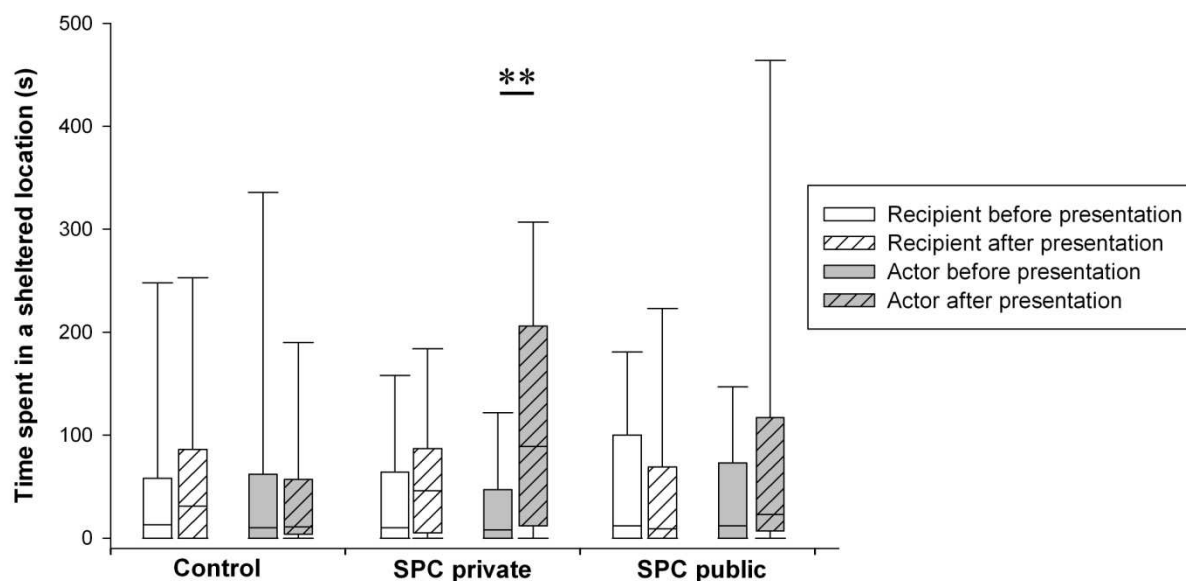
Figure 4. Time spent in sheltered locations in 10-min observation periods before and after cue presentations for the actor and the recipient in the control, the SPC private and the SPC public treatment. Median, interquartile ranges and 95 percentiles are plotted (N=19). Double asterisks represent p-values < 0.01

Movement and spatial cohesion

The proximity to the closest individual did not change for the actor or the recipient in any of the treatments when comparing the pre- and post-cue behaviour (Tab. 3). The distance moved, however, increased significantly for the actor in the control treatment (but not for the recipient in the same treatment; Tab. 3). In contrast, the distance moved did not differ for any individual in the SPC private and SPC public treatments (Tab. 3).

Table 4. Mean proximity to the closest individual in the group as an estimate of spatial cohesion and the mean distance moved during the 10-min observation period before and after cue presentations. For all tests, the sample size, the effect size and the p-value are displayed (if significant in bold).

			Median			Wilcoxon test statistics	
			Before	After	N	Effect size (Z)	P-value
Proximity	Control	Recipient	2.50	2.50	19	-0.33	0.74
		Actor	2.33	3.17	19	-1.11	0.27
	SPC private	Recipient	2.17	2.17	19	-0.56	0.57
		Actor	2.43	2.25	19	-0.54	0.59
	SPC public	Recipient	2.50	2.40	19	-0.62	0.54
		Actor	2.43	2.67	19	-0.55	0.59
Distance moved	Control	Recipient	5.80	5.40	19	-0.46	0.64
		Actor	4.29	6.40	19	-2.13	**0.03**
	SPC private	Recipient	4.00	5.20	19	-1.11	0.27
		Actor	4.20	4.60	19	-0.89	0.38
	SPC public	Recipient	6.00	5.60	19	-0.28	0.78
		Actor	6.00	6.20	19	-0.02	0.98

Number of contact calls

The contact call rate did not differ in any of the treatments, but calling frequency by the actor tended to decrease in the SPC public and SPC private treatments, and by the recipient in the control (Tab. 4).

Table 5. The total number of contact calls given during the 10-min observation period before and after the cue presentations. For all tests, the sample size, the effect size and the p-value is displayed.

			Median		Wilcoxon test statistics		
			Before	After	N	Effect size	P-value
Contact calls	Control	Recipient	8	4	19	-1.52	0.13
		Actor	7	5	19	-0.63	0.53
	SPC private	Recipient	7	2	19	-0.66	0.51
		Actor	5	3	19	-1.70	0.09
	SPC public	Recipient	5	2	19	-0.60	0.55
		Actor	8	5	19	-1.71	0.09

Guarding activity of the group

The guarding activity in the eight meerkat groups did not change significantly in the three different treatments based on scan sampling (Tab. 5).

Table 6. Guarding in the group based on the scan protocols. Group was included as a factor. The sample size therefore reflects the number of tested groups (N=8).

		General Linear Models		
	df	Mean squares	Effect size (F)	P-value
Control	1	0.27	1.42	0.26
Control * Group	7	0.22	1.14	0.41
SPC Private	1	0.42	1.31	0.28
SPC Private * Group	7	0.14	0.43	0.86
SPC Public	1	0.02	0.12	0.73
SPC Public * Group	7	0.27	1.50	0.27

Discussion

Our results demonstrate that the time spent foraging after the presentation of a secondary predator cue was reduced and, as predicted, anti-predator behaviour increased. In the "SPC public" treatment the meerkat that detected the cue was allowed to recruit and hence informed its group members. Thus, both the actor and the recipient decreased the total time spent foraging. These results suggest that all group members reduced their foraging time in response to the secondary predator cue encounter. This effect is independent of being recruiter (actor) or being recruited (recipient). The anti-predator behaviour largely showed the expected, reverse pattern to foraging. This reflects the trade-off between the two behaviours. In the SPC public treatment, both actor and receiver spent more time engaged in anti-predator behaviour. Furthermore, vigilance behaviour, which is a major component of anti-predator behaviour, increased significantly. Animals have been shown to increase vigilance or anti-

predator behaviour as a consequence of magnified predation risk (Lima and Dill 1990) or by attending to secondary predation cues (Apfelbach et al. 2005; Berger et al. 2001; Dalesman et al. 2006; Ferrari et al. 2006; Lohrey et al. 2009; Roth et al. 2008; Shrader et al. 2008). Anti-predator behaviour in general and vigilance behaviour in particular have been suggested to increase survival chances in birds and mammals (Dickman 1992; Fitzgibbon 1989; Lima and Bednekoff 1999; Lima and Dill 1990). For meerkats that encountered a secondary predator cue but did not spot a predator, it possibly pays off to increase anti-predator behaviour in the first minutes of foraging.

A more detailed examination of the foraging behaviour revealed no evidence that the meerkats switched foraging tactics in the SPC public treatment. The ratio of more risky digging behaviour (reduced visibility) to the less risky scratching/searching behaviour (Clutton-Brock et al. 1999b) did not differ significantly before and after cue presentation. Furthermore, neither the duration of searching food/scratching surface nor of digging changed significantly after a successful recruitment in response to a secondary predator cue. These results suggest that meerkats do not adjust their foraging behaviour by shifting to lower risk behaviours in higher risk situations, but rather increase anti-predator behaviour at the cost of reduced foraging time.

Although voles, for instance, reduce predation risk by reducing activity (Norrdahl and Korpimaki 1998) and diminish locomotion and activity as a reaction to predator odours (Borowski 1998), we did not find any effect of secondary predator cues in the SPC public treatment on the distance the meerkats moved or on group cohesion.

Similar to the SPC public treatment, the actor foraged less in the SPC private treatment. In the latter treatment the focal animal inspected a secondary predator cue but experimental playback hindered recruiting group members. Hence, the group did not perceive the signal of potential danger. The recipient that represented the group's behaviour continued foraging and did not change its feeding duration in the subsequent foraging session.

Analysing the actor's behaviour in the SPC private treatment, where recruitment is disabled, and SPC public treatment, where recruitment was successful, revealed a decrease in foraging time in both treatments. The effect size of the observed behavioural change is very similar in SPC private and SPC public (Foraging duration: T=3.534 and T=3.173, Anti-predator behaviour: T=-2.874 and T =-3.278); directly testing the differences showed no difference suggesting that the time invested in anti-predator behaviour and the foraging duration were independent of the successful recruitment of group members.

These results contrast with the expectation that the actor would show higher levels of anti-predator behaviour in the SPC private treatment. Through recruiting, the knowledge about the current high-risk situation becomes public in the group, and due to the overall increase in anti-predator behaviour, the

risk of being predated is diminished. Consequently, the actor itself benefits from a decreased predation risk. Furthermore, the actor could also benefit from the reduced predation risk for its group members through group augmentation (Kokko et al. 2001; Krause and Ruxton 2002) and through kin selection because meerkat group members are often close kin (Clutton-Brock et al. 2001). In this case, recruitment to secondary predator cues would be a cooperative behaviour: it is beneficial for the recipients and thus selected for in the (West et al. 2007). Apart from these benefits in a subsequent foraging session, it has been shown that all group members enjoy the advantages of early predator detection due to the reaction to secondary predator cues (Zöttl et al. Unpubl. data).

We can reject the interpretation that the actor is incapable of adjusting its behaviour to the failed recruitment because the actor did spend significantly more time in sheltered places (in and around logs, boltholes or in big bushes, also see appendix) in the SPC private versus the SPC public treatment. Possibly, this behavioural adaptation enabled that individual to balance foraging time and anti-predator behaviour in a high-risk situation. Moreover, this change in habitat use during foraging potentially incurs costs for the meerkat due to the reduced freedom of choice of preferred habitat. It has been argued that meerkats benefit energetically from foraging at the base of bushes (Thornton and Hodge 2008). Nonetheless, although big bushes can represent shelter for meerkats (Manser et al. 2001), our definition of a sheltered place (see Appendix) differs considerably from Thornton and Hodges' definition.

Interestingly, the actor's vigilance behaviour did not differ in the SPC private treatment, in contrast to the actor and the recipient in the SPC public treatment. This suggests that even though the total duration of the actor's anti-predator behaviour did not differ in the two treatments, the components of anti-predator behaviour contributed to different extents. Vigilance behaviours are defined as those that enable prey species to detect, localize or identify a predator (Apfelbach et al. 2005). They often correlate positively with predation risk (Lima and Dill 1990; Verdolin 2006). Surprisingly, we found no significant changes in the different components of vigilance behaviour, with the exception of the actor's guarding duration in SPC public. Merging all anti-predator behaviours (including rare events like "lying vigilant" and rare but mostly long behaviours like "raised guarding") might give a clearer picture of the changes in anti-predator behaviours. Anti-predator behaviours influence each other and should not be regarded completely independently. Scanning, for instance, most common during foraging, had a high frequency but a short average duration. Moreover, a meerkat exhibiting raised guard never performed scanning. When analysing both behaviours independently, we possibly miss patterns that could actually be found when focusing on time budgets and merging the total duration of different anti-predator behaviours. For this reason we think that the analyses of time investment in broadly defined anti-predator behaviours is the best proxy of costs incurred to an individual.

Crucially, we did not find a significant change in foraging behaviour in the unmanipulated recipient in either the SPC private or in the control treatment. That the presentation procedure (leading away, feeding a scorpion) did not influence the actor's behaviour is confirmed by the fact that the actor showed no significant behavioural changes after cue presentation. An exception is that the actor moved further distances after control cue presentations.

Since times of increased danger might also challenge group coordination more, it would be possible to find an effect on contact all number. Our data, however, showed no significant alterations of the contact call rate. Consequently, we cannot support the idea that meerkats react to secondary predator cues with a change in calling frequency. Similarly, guarding behaviour in the whole group does not differ between the treatments (based on the data from scan samples).

The number of alarm calls during foraging after the cue presentation did not differ between the treatments. This suggests that random predator encounters are not responsible for the pattern we found. This assumption is further confirmed by the fact that actor and recipient reacted differently in the SPC private treatment. As a result we can rule out any ecological influence as an alternative explanation for the differences in foraging and anti-predator behaviour: the experimental design ensured that the factors predators, vegetation, time during the day and seasonality always acted alike on actor and recipient.

Our results clearly demonstrate that meerkats are able to assess current danger of predation by attending to secondary predator cues, and subsequently adjust anti-predator and foraging behaviour accordingly. Regarding costs and benefits of communication about the perceived level of danger, we suggest that both actor and recipient gain through increased safety due to increased anti-predator behaviour. This underlines the importance of mutual benefits in this cooperative system. Moreover, actor and recipient face similar costs as a consequence of reduced foraging time. However, the actor did not experience higher costs in terms of reduced foraging time when recruitment was disabled. Accordingly, the clearly selfish benefit of more foraging time due to communication is unlikely to be the driving selective force behind recruitment.

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Appendix: Ethogram used for analyses.

Behaviour	Description	Merged Group	Characteristics
digging	using both forepaws at the same spot for more than 10 seconds	Foraging behaviour	state
scraching/searching food	moving in slow pace with head directed towards the ground, scratching the surface or scratching for less then 10 seconds at the same spot	Foraging behaviour	state
handling/eating prey	eating without scanning the surroundings; handling big prey	Foraging behaviour	state
being below	being in a bolthole or a burrow	Anti-predator behaviour	state
burrow renovations	digging in the bolthole/burrow entrance with both forepaws	Anti-predator behaviour	state
inspecting bolthole	looking into the burrow/bolthole entrance	Anti-predator behaviour	state
lying vigilant	laying with the whole body on the ground; head off the ground and scanning the surroundings	Anti-predator behaviour	state
raised guard	standing on two legs in an upright position more than 10 cm above the ground	Anti-predator behaviour	state
standing guard	standing on two legs in an upright position on the ground or on an object less that 10 cm above the ground; sitting in an upright position	Anti-predator behaviour	state
scanning	standing on 4 legs while scanning the surroundings	Anti-predator behaviour	state
allogrooming	grooming or scratching another group member	Neutral behaviour	state
eating vigilant	eating while scanning the surroundings	Neutral behaviour	state
lying	laying with the whole body on the ground; including the head	Neutral behaviour	state
marking	anal marking, rubbing the body or biting into vegetation	Neutral behaviour	state
other behaviour	all behaviours not mentioned in the list	Neutral behaviour	state
out of sight	being out of sight for the camera without audio protocol supplying information what the focal animal is doing	Neutral behaviour	state
running	moving in fast pace	Neutral behaviour	state
self grooming	grooming or scratching the own body	Neutral behaviour	state
social interaction	foraging competitions with group members, mating chasing other group members	Neutral behaviour	state
walking	moving in slow pace with elevated head position; head not directed to ground	Neutral behaviour	state
contact call	contact calls		event
sheltered	being in a bolthole or a burrow or in its entrance; under in or around log; under big bushes which provide shelter		state
unsheltered	being in the open or under small bushes that provide no shelter		state

Curriculum Vitae

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Conferences

2007 ESEB: "Female wing patch predicts pairing status in collared flycatchers (*Ficedula albicollis*)", Uppsala, Sweden (poster presentation)

Grants and awards (all of competitive character)

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2007 Joint Study grant

2007 ERASMUS Stipend

2006 Award for excellent study success ("Leistungstipendium")

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July - Aug 2007   Internship: Uppsala University

"Female Wing Patch predicts pairing status in Collared Flycatchers (*Ficedula albicollis*)" Supervisor: Anna Qvarnström

May – June 2007   Field assistant: The Flycatcher Project, Baltic Island Öland

Jan - Oct 2007   Student: Department of Animal Ecology, Uppsala University

2005 - 2007	Research assistant: Konrad Lorenz Institute for Ethology
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Dec 2006	Internship: Konrad Lorenz Research Station Project
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Aug 2006	Internship: Island biogeography, University of Vienna and University of Bogor (Indonesia)
2003 – pres	Student: General Biology, University of Vienna
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Scientific Skills and Qualifications:

- Computing skills in SPSS, JMP, Excel and Access
- Working with large data basis (e.g. Flycatcher database with more than 10 000 breeding attempts over the last 25 years)
- Experience in experimental work in mammals and birds (Meerkats, House mice, Flycatchers and Bald Ibis)
- Handling and blood sampling mammals and birds (House mice and Flycatchers)
- Capture-mark and recapture techniques (House mice)
- Bird ringing experience

Non academic occupations

2005 to 2007	Part time employee (20%) at the Zoo Vienna (Teaching Section)
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