Communication in the yellow mongoose, *Cynictis penicillata*

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Declaration

I, the undersigned, hereby declare that the work contained in this dissertation is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

Signature: …………………………….

Date: ………………………………

SUMMARY

Improved anti-predator protection has been postulated to be the primary advantage of sociality in the family Herpestidae. Therefore, the yellow mongoose, *Cynictis penicillata,* is considered an anomaly in the family because it may den socially with conspecifics, cooperating in the rearing of young and territory defence, but inevitably forages alone. I studied the communicative and anti-predator behaviour of a population of yellow mongooses which exhibited a lower degree of sociality than populations studied elsewhere. The yellow mongoose's flexible social nature was evident in its vocal repertoire. Although its vocal repertoire was smaller and less context-specific than those of social mongooses, it had a large proportion (over 50%) of affiliative vocalizations, suggesting that individuals show a higher degree of cooperation than strictly solitary species. During predator encounters yellow mongooses used a simple urgency-based alarm call repertoire, indicating high and low urgency threat with two separate call types. The social environment strongly affected the alarm communication of yellow mongooses – vocal alarms were displayed almost exclusively by individuals in a group, whereas the visual alarm (a raised tail) was displayed by solitary individuals, when predators were outside the range from which they were potentially dangerous. This was a clear demonstration of the 'audience effect' – a phenomenon whereby animals adjust their communicative signals depending on the audience that is present. Until this study, the audience effect has only been demonstrated in obligate social species. The yellow mongoose's social flexibility was further reflected in its territorial scent marking behaviour. In contrast to high density populations, where subordinate individuals contribute significantly to territory defence and scent marking, only the dominant male marked and defended territory borders in this low density population. Dominant males appeared to overmark the small number of cheek marks that females deposited, especially during the breeding season, which suggests that cheek marks were used in mate guarding. The yellow mongoose showed less flexibility in responses to conspecifics while foraging: the presence of group members appeared to make foragers more nervous, as individuals increased vigilance and decreased foraging success when group members were nearby. This could not be attributed to foraging competition, which happened very rarely. Yellow

mongooses relied on a form of vigilance that allowed them to continue foraging while remaining alert, which contrasted with meerkats, *Suricata suricatta,* that had to interrupt foraging in order to be vigilant. The foraging patterns of yellow mongooses and meerkats differed markedly, and both species appeared to be inflexible in these patterns. I have proposed, therefore, that rigid vigilance patterns of vigilance are the reason why yellow mongooses forage alone, despite showing other cooperative tendencies. This study highlights that the selective forces acting on group living and group foraging are very different, and that the group-size effect – which postulates that individual vigilance declines as group size increases – may not be applicable to species adapted to solitary foraging.

OPSOMMING

Die stelling word dikwels gemaak dat verbeterde verdediging teen roofdiere die hoof voordeel is van groepslewe in die familie Herpestidae. Die geelmuishond, *Cynictis penicillata,* word dus as 'n uitsondering beskou, aangesien hulle in groepsverband saambly, gesamentlik kleintjies grootmaak en hul territorium verdedig, maar alleen kossoek. Ek het die geelmuishond se kommunikasie en roofdier ontduiking bestudeer in 'n populasie met 'n laer graad van sosialiteit as dié wat al elders bestudeer is. Die geelmuishond se buigsame sosiale aard was duidelik vanuit sy vokale repertoire. Hoewel hul repertoire kleiner en minder verband-spesifiek was as dié van sosiale muishonde, het dit 'n groot verhouding (meer as 50%) vriendskaplike roepgeluide gehad. Dit dui aan dat die geelmuishond 'n hoër vlak van samewerking toon as suiwer alleenlopende species. Tydens ontmoetings met roofdiere het geelmuishonde 'n eenvoudige dringendheids-gebaseerde alarmroepstelsel gebruik, wat hoë en lae vlakke van gevaar aangedui het deur middel van twee verskillende geluidtipes. Die sosiale omgewing het die geelmuishond se kommunikasie sterk beïnvloed – alarm roepgeluide was amper uitsluitlik deur individue in groepsverband gebruik, terwyl die visuele alarmteken ('n opgeligde stert) deur alleenlopende individue gebruik is, wanneer roofdiere op 'n steeds veilige afstand was. Dit was 'n duidelike voorbeeld van die 'toeskouer effek' – 'n fenomeen waartydens diere hul kommunikasietekens aanpas afhangend van die gehoor wat teenwoordig is. Totdat hierdie studie gedoen is, is die toeskouer effek slegs in hoogs sosiale species bewys. Die geelmuishond se sosiale buigsaamheid was verder ook in sy gebiedsmerkingsgedrag te bespeur. In teenstelling met hoë-digtheidspopulasies, waar ondergeskikte individue betekenisvol bygedra het tot gebiedsverdediging en reukmerke, het slegs die dominante mannetjie in hierdie lae-digtheidspopulasie die territorium se grense verdedig en gemerk. Dominante mannetjies het oënskynlik die wyfies se klein aantal wangmerke oorgemerk, veral gedurende die broeiseisoen, wat 'n aanduiding van moontlike paarmaat-afskerming is. Die geelmuishond het minder aanpasbaarheid getoon in sy gedrag teenoor groepslede tydens voedingsekskursies: die teenwoordigheid van groepslede het ander individue oënskynlik senuagtig gemaak, aangesien hulle waaksaamheid toegeneem en voedingsukses afgeneem het terwyl groepslede in die nabyheid was. Dit kon nie

toegeskryf word aan voedingskompetisie nie, aangesien hierdie gedrag baie selde waargeneem is. Geelmuishonde het gebruik gemaak van 'n vorm van waaksaamheid wat hulle toegelaat het om aan te hou kossoek terwyl hulle waaksaam bly. Dit was merkbaar verskillend van die waaksaamheidsgedrag van meerkatte, *Suricata suricatta*, wat voeding moes onderbreek om die wag te kon hou. Hierdie twee species blyk rigied te wees in hul onderskeie waaksaamheidspatrone. Ek het dus voorgestel dat die onbuigsame waaksaamheidspatroon van die geelmuishond die rede is waarom hulle altyd alleen kossoek, selfs al toon hulle ander samewerkende neigings. Hierdie studie lig uit dat die selektiewe kragte wat op groepslewe inwerk, sterk kan verskil van die kragte wat selekteer vir sosiale kossoek gedrag. Die groepsgrootte effek – wat aandui dat individuele waaksaamheid afneem soos wat groepsgrootte toeneem – is dus nie noodwendig van toepassing op species wat aangepas is vir enkellopende kossoek gedrag nie.

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CHAPTER ONE

GENERAL INTRODUCTION

Helen Eaton

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Marler (1961) and Wilson (1972) suggested that social complexity can predict communicative complexity: systems of communication will become elaborated only in social species, whereas more solitary species will rely primarily on brief, simple communicative signals. In mammals, trends appear to support the hypothesis. Larger signal repertoires are found in species with large, stable groups and a high degree of intragroup cooperation, whereas less gregarious species have smaller repertoires, whether vocal (marmots, genus *Marmota*, Blumstein & Armitage 1997; Mustelidae, Wong et al. 1999; Chiroptera, Wilkinson 2003) or visual (Canidae, Kleiman 1967). However, rigorous comparative tests of this hypothesis, such as McComb and Semple's analysis of primate vocalizations (2005), have been hampered by a lack of comprehensive data on communication in nongregarious species. As the vocal repertoires of less social mammals sometimes reveal surprising complexity – for example, in the coyote, *Canis latrans* (Kleiman & Brady 1978) and Garnett's greater bush baby, *Otolemur garnettii* (Becker et al. 2003) – it is important to obtain more complete descriptions of communication in species that do not live in cohesively social groups. In this thesis I focus on the communicative repertoire of a solitary foraging carnivore, the yellow mongoose, *Cynictis penicillata* (Taylor & Meester 1993). This is a species with a flexible social environment and I attempt to determine how its sociality affects its visual, vocal and olfactory signalling behaviours. As sociality in mongooses is strongly linked to anti-predator defence (Rood 1986), I also investigate the possible effects of the yellow mongoose's flexible sociality on its anti-predator behaviours. This includes a comparison of the yellow mongoose's vigilance behaviour with the sympatric, obligate social meerkat, *Suricata suricatta*, a mongoose with complex communication (Manser 2001) and anti-predator defences (Graw & Manser 2007).

1.1. SOCIALITY

1.1.1. Social Systems Defined

As intraspecific variation in vertebrate social systems is the rule rather than the exception (Bekoff et al. 1984; Lott 1991), and, within a species, there may even be marked social

differences between the two sexes (Eisenberg 1981), the categorization of a species' lifestyle as either strictly solitary or social is too restrictive. A social group or 'society' (Wilson 1975) is a group of conspecifics gathered in a cooperative manner, in contrast to an aggregation, which is simply a temporary gathering of conspecifics around a common resource, such as snow hares, *Lepus americanus,* gathering around food (Quenette et al. 1997). A species' social system can be described as an integration of the levels of cooperation shown by individuals during the four functional phases of their lives, i.e. (1) mating, (2) rearing, (3) foraging, and (4) refuging (Eisenberg 1981). Depending on the degree of cooperation individuals exhibit during all these phases of their lives, a species' social system or 'degree' of sociality can be placed somewhere along an 'eusociality continuum' (Sherman et al. 1995), with solitary species at one end and eusocial species at the other. Cooperatively breeding species such as wild dogs, *Lycaon pictus* (Estes & Goddard 1967), and dwarf mongooses, *Helogale parvula* (Rasa 1989b), show a division of labour within the group and cooperation in all four functional phases, which may enhance foraging success or the inclusive fitness of all group members (West Eberhard 1975; Gaston 1978). This labour division is not found in the temporary groupings of solitary species but can reach such extremes in eusocial species that the helping 'castes' forego reproduction completely (Crespi & Yanega 1995).

1.1.2. Causes and Consequences of Sociality

As every organism basically attempts to maximize its reproductive success during its lifetime, there is a need to explain why individuals would live co-operatively with conspecifics, and thus hamper or delay their own reproduction. Individuals living in social groups compete for mating and foraging opportunities, vie for dominance positions, are more susceptible to parasite-transmission and, because of larger numbers, become more visible to predators (Alexander 1974; Poole 1985). The selective forces allowing group living to develop are relatively few, and appear to be limited to the distribution and abundance of resources, which comprise shelter, food, and mates (Alexander 1974). If these resources are sufficiently abundant or scarce enough to make conspecific tolerance more beneficial than intolerance, group-living will be favoured.

Male raccoons, *Procyon lotor*, for example, are social due to local female abundance (Gehrt & Fritzell 1998), whereas the scarcity of sleeping burrows has led to the development of sociality in hystricognath rodents (Ebensperger & Blumstein 2006). In all cases, food must be abundant or renewable enough to support a higher number of conspecifics within a given area, and food dispersion has had a powerful effect on the development of sociality (Waser 1981; Johnson et al. 2002). The effect of local food abundance and food choice can lead to variation in the sociality exhibited by solitary as well as social species. In some solitary species, such as foxes, *Vulpes vulpes* (White et al. 1996), and the slender mongoose, *Herpestes sanguineus* (Rood 1989), groups forage socially where human disturbance has led to local food abundance. Occasionally, sociality may develop due to same-sex coalitions (e.g. Cape ground squirrels, *Xerus inauris*: Waterman 1997), but in many social mammals, group-living has developed due to natal philopatry (Canidae and Felidae, Kleiman & Eisenberg 1973; Sciuridae, Armitage 1981; voles, *Microtus* spp., Boonstra et al. 1987), where offspring stay behind in their natal territories beyond the age of reproductive maturity.

Resource dispersion may allow group-living to develop (Johnson et al. 2002), but there are different factors which will *promote* the evolution of cohesively social groups – the primary factor being improved anti-predator defence. Individuals in a group derive several anti-predator benefits from the effect of sheer numbers. A prey animal in a group has a 'diluted' risk of being successfully attacked, simply by being amongst many prey animals (Hamilton 1971), a benefit that is especially evident in large groups of animals (Delm 1990). Individuals in a group may also become aware of a predator's presence earlier than solitary animals, purely because there are other individuals around that could help detect predators (Pulliam 1973). In addition, a large group of prey animals scattering and running at the same time may confuse a predator, and thus thwart successful attack (Vine 1971; Landeau & Terborgh 1986). These numerical benefits – the 'group-size effect' – have been shown in a variety of avian and mammalian taxa (Elgar 1989; Quenette 1990), where individuals in larger groups spend less time on vigilance and consequently have more time to forage than individuals in smaller groups. In most social species, these anti-predator benefits are maximized through alarm signaling behaviour and communal defence (Klump & Shalter 1984; Lima & Dill 1990).

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1.1.3. Social Systems in Mammals

As reviewed by Eisenberg in 1981, most mammals fall somewhere in between the two social systems at the extreme ends of the eusociality continuum. Whereas the ancestral mammals were solitary, there are cohesively social species in most mammalian families (Eisenberg 1981). Eusociality is rare in mammals, displayed only by naked mole rats, *Heterocephalus glaber* (Lacey & Sherman 1997; Burda et al. 2000), and is characterized by a social system of reproductive altruism, with only one female performing all the reproduction, a large overlap of adult generations, and lifelong philopatry of non-breeding individuals that help raise the female's offspring. Solitary mammals exhibit some degree of cooperation because all female mammals suckle their young, implying a period of maternal care in even highly solitary species (Eisenberg 1981). In a few solitary species one of the two sexes exhibits a different degree of sociality from the other; for example male cheetahs, *Acinonyx jubatus,* (Caro 1994), raccoons (Gehrt & Fritzell 1998) and slender mongooses (Waser et al. 1994), form coalitions, whereas the females remain solitary. Some mammals, including several nocturnal prosimians (Müller & Thalmann 2000), and rodents such as the striped mouse, *Rhabdomys pumilio* (Schradin & Pillay 2004), are 'solitary foragers.' Solitary foragers do not forage in groups, but exhibit cooperative behaviours at sleeping sites (e.g. Schradin & Pillay 2004; Braune et al. 2005) and are therefore not strictly solitary, even though they are frequently seen as such (Müller & Thalmann 2000). Yellow mongooses, denning in groups, but foraging alone, may be considered solitary – or, at best, 'pair' – foragers (Nel & Kok 1999). Obligate social systems, as found in, e.g. wild dogs, *Lycaon pictus* (Creel & Creel 1995), various primates (Müller & Thalmann 2000) and elephants (Payne 2003), are characterized by, *inter alia*, cohesive group movement during foraging, mutual grooming that maintains social bonds and, often, alloparental care of offspring. In many of these systems – such as communally breeding carnivores (MacDonald & Moehlman 1982) – dominant individuals suppress the reproduction of subordinates. The costs and benefits of group living in mammals are regulated by various behaviours, most of which involve visual, vocal and olfactory communication (Poole 1985).

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1.2. COMMUNICATION

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1.2.1. Communication Defined

In 'true communication' (Marler 1968; Bradbury & Vehrencamp 1998) both sender and receiver try to maximize signal transmission, and the sender or both individuals usually benefit from such communication. True communication can be distinguishing from inadvertent communication (Marler 1968; Bradbury & Vehrencamp 1998), which happens when only the receiver benefits from cues emitted by the sender, and the sender tries to minimize signal transmission to this 'eavesdropping' receiver. Male African lions, *Panthero leo,* for example, refrain from roaring when traveling through other males' territories, in order to hide their presence from residents that could eavesdrop on their loud signals and may attack them (Grinnell & McComb 2001). In all communicative modalities, signal structure is affected by sender and receiver physiology and psychology as well as the biotic and abiotic environment (Otte 1974; Ehret 1987; Guilford & Dawkins 1991; Alberts 1992; Endler 1992). Signal repertoires are affected by above factors, and also, potentially, the sender's social environment.

1.2.2. The Social Environment

1.2.2.1. The communicative repertoire

As the exchange of information is the basis for the regulation of social interactions (Eisenberg 1981), communicative signals are expected to be well-developed in gregarious species that experience a high frequency of social interactions. The sensory systems of mammals are closely integrated and very little mammalian communication takes place in only a single modality at a time (Eisenberg 1981). Therefore, a species' entire communicative repertoire – defined by Bradbury and Vehrencamp (1998) as the suite of distinct signals used by a species – is potentially affected by the number of social interactions in which individuals are typically engaged. Schassburger (1993) predicted an increase in (1) the size of the communicative repertoire; (2) the context-specificity of

signals; and (3) the proportion of affiliative signals in the repertoire, as degree of sociality increases. Although he was specifically discussing the vocal repertoire of canids (Schassburger 1993), these predictions are potentially applicable to all communicative systems used by mammals. Solitary and social mammals use signals in territory defence, sexual advertisement and competition, during mother-offspring interactions, and occasionally to mark food caches/ sites (Poole 1985; Bradbury & Vehrencamp 1998). In addition, social animals use signals in several contexts to which solitary species are never exposed. To minimize the costs of group-living, communication is necessary to reduce intragroup conflict and maintain dominance hierarchies without constant costly attacks (Craig 1921; Moynihan 1998). Socially foraging species use signals to coordinate group movement (Stewart & Harcourt 1994; Boinski & Campbell 1995) and vigilance (Wickler 1985; Rasa 1986), and to communicate the presence of predators to conspecifics (Maynard Smith 1965; Sherman 1977). The unique properties of the various communicative modalities make some of them more useful to solitary species, and others, to social species.

1.2.2.2. The audience effect

Individuals adjust their observable behaviour depending on the presence or absence of specific group members. For example, the sexual behaviour of subordinate Merino rams is inhibited by the mere presence of dominant males, which Lindsay and his colleagues (1976) described as an 'audience effect'. This phrase, since then, has been applied largely to communicative behaviour – i.e. individuals adjust their communicative signals depending on the presence or absence of conspecifics. Such an audience effect has been explicitly demonstrated in numerous vertebrates in the context of alarm signaling (Karakashian et al. 1988; Wich & Sterck 2003), calls announcing food discovery (Marler et al. 1986; Evans & Marler 1994; Dahlin et al. 2005; di Bitetti 2005), and mating displays (Doutrelant et al. 2001; Vignal et al. 2004; Dzieweczynski et al. 2005). In addition, from other studies, it can be inferred that signaling is affected by the nature of the audience. Black-tailed prairie dogs, *Cynomys ludovicianus* (Hoogland 1983), and Belding's ground squirrels, *Spermophilus beldingi* (Sherman 1977), for example, give

more alarm calls when surrounded by kin rather than non-kin. Killer whales, *Orcinus orca*, suppress their usual vocal behaviour while hunting, as their mammalian prey can potentially detect their signals and escape (Deecke et al. 2005). Examples of behavioural deception in social species such as baboons, *Papio ursinus* (Byrne & Whiten 1985), also suggest that signallers are highly aware of the potential receivers of their visual signals. The audience effect is ubiquitous in all species in which it has been studied, and is a logical consequence of true communication, as senders can be expected to be aware of their signals' potential receivers. However, the audience effect has been studied only in social species, and this phenomenon still needs to be investigated in less gregarious mammals.

1.2.3. Chemical Signals

1.2.3.1. Characteristics

Communication through chemical signals is important for most mammals (see reviews in Ralls 1971; Eisenberg & Kleiman 1974; Brown 1979; Gorman & Trowbridge 1989). As products of glandular secretion, bacterial fermentation, and the process of digestion, chemical signals can be produced only in limited quantities at a time, and therefore they are subject to economical considerations (Alberts 1992). Chemical signals, such as scent marks, are typically long-lasting and degrade over a longer period than other types of signals (Wilson 1968; Bradbury & Vehrencamp 1998), making it the ideal modality for communication in solitary species, as sender and receiver do not need to be present simultaneously for communication to take place. Chemical signals are often individually distinct, allowing olfactory recognition of familiar individuals or kin discrimination in many species (Brown & Eklund 1994; Heth & Todrank 2000; Mateo 2002). Carrying relatively long-lasting cues of identity, the primary functions of scent marks involve the advertisement of (1) dominance within a group and/ or territory, and (2) sexual status.

1.2.3.2. Territoriality

The occupants of a territory – whether a single individual or a group – typically scent mark their territory borders to advertise ownership, with the dominant individual usually contributing the most to these marks (Ralls 1971; Eisenberg & Kleiman 1974). Scent marks are most often left at the territory borders (Sillero-Zubiri & MacDonald 1998; Brashares & Arcese 1999b) but when the territory border is too long for an individual or group to mark regularly, the 'hinterland' marking strategy is employed (Gorman & Mills 1984). In the hinterland strategy marks are primarily deposited in the territory core, with radiating 'arms' of scent marks around the core (e.g. in gerenuk, *Litocranius walleri*, Gosling 1981; and honey badgers, *Mellivora capensis*, Begg et al. 2003). This pattern appears to maximize the chances of an intruder encountering scent marks before reaching the centre of the territory. Although territorial scent marks have been interpreted as creating a 'wall of smell' that aggressively keeps out intruders – the 'scent fence' hypothesis (Gosling 1982) – scent marks alone are seldom enough to deter intruders (e.g. in beavers, *Castor canadensis*: Sun & Müller-Schwarze 1998). Gosling (1982) proposed the 'scent matching' hypothesis of territorial demarcation, suggesting that intruders familiar with the scent marks deposited by territory owners would be able to identify the owner, based on scent, when they encounter him. If ownership is thus established, the intruder would retreat without a costly fight, as owners are highly likely to win any physical contest. This hypothesis has been supported in some subsequent studies in the field (Sun & Müller-Schwarze 1998; Luque-Larena et al. 2001) and the laboratory (Gosling & McKay 1990) but rejected in others (Richardson 1991; Brashares & Arcese 1999a; Begg et al. 2003). The studies that rejected the scent match hypothesis indicated that intrasexual competition drives scent marking patterns, as territory owners mark more often at borders where there are more male competitors (Brashares & Arcese 1999a). Richardson (1991) argued that territorial scent marks are not simply informational in value, but convey a threat of attack – the more marks, and the fresher the marks, the more likely it would be that an intruder will be attacked. As females also prefer the scent of males that marked over the scent of another male (Johnston et al. 1997; Rich & Hurst

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1999), the regular maintenance of territorial scent marks is, additionally, important in sexual advertisement.

1.2.3.4. Sexual advertisement

Solitary as well as social mammals use chemical signals for sexual advertisement during the breeding season (Blaustein 1981), leaving marks in locations where they are likely to be encountered by conspecifics (Kappeler 1998; Thomas & Kaczmarek 2002; Begg et al. 2003). Females often advertise their reproductive status through olfactory signals, and males of a number of species have been shown to prefer the scent of estrus to anestrous females (Eisenberg & Kleiman 1974). Whereas olfactory signs of estrus are often conspicuous (Eisenberg & Kleiman 1974), in some mammals, such as pygmy marmosets, *Cebuella pygmaea* (Converse et al. 1995), these signals can be very subtle and only males in close attendance to the female will be made aware of her ovulatory state. By overmarking a female's scent, dominant males could perform mate-guarding (e.g. in klipspringers, *Oreotragus oreotragus*: Roberts & Dunbar 2000; and Verreaux's sifaka, *Propithecus verreauxi verreauxi*: Lewis 2005), through masking the olfactory cues of her reproductive state from competitors.

1.2.3.5. Influence of the social environment

Sources of odour are morphologically constrained in both social and solitary species, so that the number of distinct signals in a species' olfactory repertoire will have an upper limit that is unaffected by sociality. The number of scent glands found in voles, *Microtus* spp, increases with level of sociality (Ferkin 2001), but this is a rare example of sociality directly affecting the size of the olfactory 'repertoire.' As summarized by Halpin (1984), scent marks serve a variety of functions in solitary as well as social species, and a simple prediction of increased scent marking rates with increased sociality may not be realistic. However, individual scent marking patterns – rate, location and intensity of marking behaviour – are affected by the social environment, and the role(s) an individual plays within a group. Typically, the dominant male in a social group reinforces his dominance

through regular scent marking, and individuals of lower status have lower scent marking rates (Ferris et al. 1987; Drickamer 2001; Miller et al. 2003). After conflicts, losing individuals will scent mark less, while winners will scent mark more, e.g. in Mongolian gerbils, *Meriones unguiculatus* (Shimozuru et al. 2006), mice, *Mus musculus* (Lumley et al. 1999), and Syrian golden hamsters, *Mesocricetus auratus* (Potegal et al. 1993). The contribution to cooperative defence also affects an individual's scent marking rate – those individuals that actively defend the territory during fights with neighbours will also mark more than others (e.g. Lazaro-Perea 2001). Females often indicate ovulatory state through increased marking rates, but in some cases of reproductive suppression, subordinate females may never increase their marking rate as ovulation is inhibited (Hradecky 1985). The role an individual plays within a social group (breeder versus non-breeder, dominant versus subordinate) therefore affects the rate of scent marking, but social interactions do not affect the scent-marking 'repertoire' in the sense of increasing the variety of distinct signals used. It is therefore probable that the scent marking patterns of a population of social mammals will be more heterogeneous than those found in a population of solitary mammals.

1.2.4 Visual Signals

1.2.4.1. Characteristics

Visual signals usually take the form of conspicuous, ritualized displays that originate in species-typical behaviours or autonomic responses (Bradbury & Vehrencamp 1998). Using tail and body movements, most mammals would communicate intent, such as readiness to fight (Eisenberg 1962), or willingness to mate (Lisk 1970), whereas facial expressions are an important aspect of visual communication in some taxa, including the primates and canids (Andrew 1963; Kleiman 1967). Autonomic responses, such as piloerection (Andrew 1963), often form part of visual displays, as do certain permanent body ornaments, such as the antlers displayed by male muntjac, genus *Muntiacus* (Barrette 1977). Dominant and submissive displays are usually the exact opposite of each other, the principle of antithesis already recognized by Darwin (1872). Dominant

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animals, for example, would bare their teeth and make themselves appear larger, whereas submissive animals would crouch and appear smaller to appease the dominant and avoid serious conflict (e.g. in deer mice, genus *Peromyscus*, Eisenberg 1962; and many canids, Kleiman 1967). As immediate and graded signals, visual signals are subject to some similar constraints and advantages of close-range vocalizations, and are potentially strongly affected by the social environment.

1.2.4.2. Interspecific communication: visual alarm signals

Although directing conspicuous signals towards a predator may seem counterproductive, many species, mammalian and otherwise, display bold visual signals when encountering predators (Stevens 2007). Whereas the majority of solitary species rely on cryptic coloration and behavioural patterns to camouflage themselves from predators (Cott 1940; Caro 2005), a number of species use bold, 'protean' (Humphries & Driver 1970) displays when they encounter predators, such as the sudden flashes of bright colour, stotting, and zigzagging flight patterns found in many ungulates (Humphries & Driver 1970; Caro 2005). These displays may confuse the predator when an entire herd of highly conspicuous animals suddenly takes flight (Vine 1971; Caro et al. 2004). Sudden, explosive flight behaviour could also momentarily startle the predator and thereby thwart attack (Humphries & Driver 1970). When predators rely on ambush hunting, prominent visual alarm displays may signal to the predator that it has been perceived, and thereby discourage pursuit (Woodland et al. 1980; Caro 1995). Smythe (1970) proposed that visual signals may deliberately invite early pursuit, encouraging the predator to start its attack before it is within the optimal attack distance range. Thus, the prey animal would thwart a successful attack. However, the evolution of 'pursuit invitation' signals has been refuted convincingly (Hirth & McCullough 1977; Coblenz 1980). Another form of visual anti-predator defence is mobbing behaviour. Mobbing behaviour can be performed by one or many animals, and mobbers may move together as a tightly-knit unit, harassing the predator and encouraging it to move on (e.g. in Siberian chipmunks, *Eutamias sibiricus*, Kobayashi 1996; and meerkats, Graw & Manser 2007)*.* A predator's attention may also be redirected to a less vulnerable body part such as a distinct tail-tip or a

flagging, pilo-erected tail (Powell 1982; Towers & Coss 1991). A final visual display that is occasionally used against predators, is feigning death, a form of defence for which opossums, *Didelphus marsupialis*, are well-known (Francq 1969). Being directed at a predator rather than conspecifics, these visual signals are affected by the predators' hunting methods and sensory systems, rather than the prey animal's social environment.

1.2.4.3. Influence of the social environment

Visual communication, relying on the close proximity of sender and receiver, is not always an important component of the communicative repertoire of solitary mammals, but serve multiple functions in the lives of social mammals that need to continually regulate and minimize intragroup aggression. In canids, for example, one of the primary differences between solitary and social species' communicative repertoires is a shift from olfactory and simple vocal communication in solitary species, to more elaborate visual and vocal signals in social species (Kleiman 1967; Poole 1985; Schassburger 1993). Specialized and complex movements of the face, body and tail in social canids, such as wolves, are used by individuals to regulate dominant and submissive interactions, or to maintain a stable dominance hierarchy (Kleiman 1967). Visual signals used in the appeasement of dominant individuals, reconciliation between group members, and the maintenance of social bonds are also well-known in social primates, that use behaviours such as lip-smacking, 'smiling' and other signals to maintain friendly relationships between group members (de Waal & van Roosmalen 1979; de Waal 1986). Marler (1968) discussed allogrooming – found in the behavioural repertoire of many social (Hart & Hart 1992; O'Brien 1993) and solitary (Baker 1984; Wiens & Zitzmann 2003) mammals – as part of the visual communication system, in which submissive individuals would quell the aggression of a dominant animal by visually soliciting mutual grooming. Although allogrooming has physiological benefits, such as a lowering of heart rate (Feh & de Mazieres 1993), it is also part of a display that communicates submission to, and appeasement of dominant individuals (Marler 1968; Bradbury & Vehrencamp 1998). Visual signaling thus appears to be affected by sociality, but no comparative studies have been conducted on the link between sociality and visual communication. Such studies are

likely complicated by the way in which visual signals are typically studied – as an entire display or 'picture' (Rosenthal & Ryan 2000). This makes the comparison of 'simple' versus 'complex' visual signals harder than, for example, vocal signals, that are typically described in terms of their discrete components (Rosenthal & Ryan 2000).

1.2.5. Auditory Signals

1.2.5.1. Characteristics

Vocalizing – in which mammals produce signals by means of the larynx and mouth (Bradbury & Vehrencamp 1998) – is the most prominent form of auditory communication in mammals. Rarer forms of auditory communication, such as the chest-beating of gorillas (Emlen 1962), form part of displays that usually include loud vocalizations. In some species, vocalizations can be used as a method of navigation by means of echolocation (autocommunication), with one individual acting as both sender and receiver of the signal (Kanwal et al. 1994; Wilkinson 2003). In this thesis I primarily address vocalizations that are used in intragroup communication. Many auditory signals carry information on individual identity, and receivers use these cues to discriminate between group members (McComb et al. 2000; Blumstein & Daniel 2004; Searby et al. 2004). Vocalizations may be used as long distance (Langbauer 2000) and short-range signals (Peters & Tonkin-Leyhausen 1999), and auditory communication can take place without the need for visual proximity. Vocal signals are highly variable and can accurately reflect grades of motivation to a very fine degree (Poole 1985; Seyfarth & Cheney 2003). Vocal signals have the capacity to reach a high level of complexity, as found in social mammals such as primates (Brinck & Gardenfors 2003; Seyfarth et al. 2005), elephants (Langbauer 2000) and dolphins (Reiss et al. 1997; Tyack 2003). Most young mammals appear to develop the correct vocal responses only over time, whether through learning or maturation (e.g. Hauser 1989; Hollén & Manser 2006).

1.2.6.2. Referential signals

Early researchers assumed that non-human animals' vocalizations are primarily indications of motivational state, reflecting a caller's anxiety, goals or needs (Smith 1965), rather than referring to external objects or abstract concepts. However, it has become clear that some animals do refer to external referents, using specific vocalizations to announce, for example, the presence of a certain type of predator (Seyfarth et al. 1980) or food (Marler et al. 1986; Evans & Marler 1994), although the motivational component of vocalizing can never be completely excluded (Seyfarth & Cheney 2003). Functionally referential signals are distinct vocalizations produced under specific circumstances, that elicit predictable responses from receivers, even in the absence of the original stimulus that had evoked the call (Macedonia & Evans 1993; Evans 1997). As such, the information contained in functionally referential signals is enough that receivers of the signal do not need to verify the context, as would happen in the case of purely motivational vocalizations (Evans 1997). Functionally referential vocalizations have been demonstrated in a number of vertebrates, including chickens, *Gallus gallus* (Evans et al. 1993a; Evans & Evans 1999), Rhesus monkeys, *Macaca mulatta* (Gouzoules et al. 1984)*,* meerkats (Manser 2001; Manser et al. 2001), and chimpanzees, *Pan troglodytes verus* (Crockford & Boesch 2003). In terms of alarm call repertoires, functionally referential signals are considered to be more complex that urgency-based calls, which reflect the level of perceived threat (Macedonia & Evans 1993). Habitat complexity strongly affects the evolution of functionally referential alarm signals, through affecting the number of escape options available to prey, and the visibility of predators. Specifically, in a more complex three-dimensional environment, prey animals that have variable escape options tend to use more complex alarm repertoires (Macedonia & Evans 1993), and the reduced visibility of predators lead to more accurate vocal indications of the exact nature of the threat (Evans et al. 1993b). In obligate social species, the need to coordinate group movement may lead to the development of functionally referential alarm signals (Furrer & Manser submitted). Although sociality favours the evolution of alarm calling itself (Shelley & Blumstein 2005), the link between the complexity of alarm call repertoires

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and sociality is not always clear, perhaps due to the strong influence of habitat complexity (Blumstein & Armitage 1997).

1.2.5.3. Influence of the social environment

The link between social and communicative complexity has been investigated mainly in vocal communication (e.g. Blumstein & Armitage 1997; McComb & Semple 2005). In part, this may be because vocal signals are relatively easy to classify into discrete components, compared to, for example, visual signals (Rosenthal & Ryan 2000), and therefore communicative complexity is more readily defined in the acoustic modality. Vocalizations are common in contexts such as conflict resolution (de Waal 2000; Aureli et al. 2002), coordination of group movement (e.g. Trillmich et al. 2004) and the regulation of vigilance behaviour (e.g. Manser 1999), to which solitary species are never exposed. Within-family trends suggesting a strong link between social and vocal complexity in mammals such as badgers (Wong et al. 1999) and bats (Wilkinson 2003) merit more rigorous investigation.

1.3. MONGOOSE EVOLUTION

1.3.1. Mongoose Social Systems

The family Herpestidae is a group of carnivores consisting of 39 species in 19 recent genera, occupying widespread areas in Africa, Madagascar, the East Indies and southern Asia (Rood 1986; Wozencraft 1989). Although most herpestid species are classified as solitary, some species form cohesive social groups with complex anti-predator defences and the cooperative rearing of young (Rood 1986; Palomares & Delibes 2000). In at least two of these obligate social species – the dwarf mongoose (Creel et al. 1993; Creel 1996) and the meerkat (O'Riain et al. 2000; Clutton-Brock et al. 2001b) – dominant individuals suppress the reproduction of subordinates and are responsible for almost all the breeding in a group. The development of sociality in the Herpestidae differs from other, large

carnivores, where communal hunting (MacDonald 1983; Creel & Creel 1995) and defence of large kills from scavengers (Vucetich et al. 2004) favour group-living. Social mongooses tend to be small and diurnal, eating invertebrate prey that do not require communal efforts to kill, and anti-predator defence appears to be the primary factor promoting and maintaining sociality in herpestids (Gorman 1979; Rood 1986). Solitary mongooses are primarily – but not always – large, nocturnal vertebrate eaters (Rood 1986; Veron et al. 2004). The presence of noisy group members will interfere with hunting success, and small prey cannot be shared communally, which is probably why vertebrate-eating mongooses tend to be solitary (Rood 1986). The ancestral mongoose species are considered to be solitary, nocturnal, forest-dwelling vertebrate eaters (Veron et al. 2004). During the Pleistocene, an increased abundance of invertebrate food resources in open areas allowed the subsequent evolution of social foraging (Waser 1981; Veron et al. 2004), and when offspring remained behind in natal territories, improved anti-predator benefits was the primary selective force maintaining sociality (Waser & Waser 1985; Rood 1986; Veron et al. 2004). Within the family there are a few solitary foraging species, such as the Egyptian mongoose, *Herpestes ichneumon,* and yellow mongoose, that forage alone but den together with conspecifics in small groups where food availability allows this (Earlé 1981; Palomares & Delibes 1993). These solitary foragers exhibit behaviours that may resemble those displayed by species directly ancestral to the social mongooses (Rood 1986).

1.3.2. Mongoose Scent Marking Behaviour

All mongooses have anal scent glands (Pocock 1916) and the family is well-known for its scent-marking behaviour (Gorman 1980). Most species are territorial and use anal gland secretions, body-rubbing, cheek gland secretions, faeces and urine to mark objects in their territories (Gorman 1980). From captive studies on social (Rasa 1973; Moran & Sorensen 1986) and solitary species (Baker 1982; 1988a; 1998) it appears as if different species use scent marks in a relatively similar way: cheek marks are short-lived signals that convey a threat message to recipients, and are left around sleeping areas (nest boxes or sleeping burrows); whereas anal gland secretions contain individual identity cues, last

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longer and act as the primary territorial marks at the borders and cores of territory areas (Rasa 1973). The signaling function of faeces, which are deposited in middens at territory cores and borders, has been studied in a wild population of the obligate social meerkat (Jordan et al. 2007). Faeces appear to serve an information exchange function, and are concentrated around sleeping burrows in the territory core and border, in locations where intruders are likely to find the signals (Jordan et al. 2007). Dominant male meerkats may use these signals in mate guarding during the breeding season (Jordan et al. 2007). In the banded mongoose, *Mungos mungo* (Müller & Manser 2007), latrines from neighbouring groups evoke a stronger vocal signaling and inspection reaction from resident groups than did latrines from an unfamiliar group, suggesting that banded mongooses treat neighbours as active threats rather than 'dear enemies' (Temeles 1994).

1.3.3. Mongoose Vocal Repertoires

Evidence suggests that the vocal repertoires of social mongooses (Mulligan & Nellis 1973; Manser 1998) are larger than those of solitary species (Baker 1982; 1988b). Solitary species' communication is focused on aggressive interactions (Baker 1982) and signals are not highly context-specific (Baker 1988b), whereas social species have a large proportion of affiliative vocalizations and vocalizations linked to group coordination and cooperative alarm responses that solitary species lack (Manser 1998). In social species, pups emit specific begging calls that elicit food-provisioning by adult helpers (Manser & Avey 2000). Contact calls – vocalizations which coordinate group movement and inter-individual distance – are part of the vocal repertoires of all socially foraging mongooses (Kingdon 1997; Mills & Hess 1997), and have been noted in the Egyptian mongoose's repertoire in an area where they foraged socially (Palomares 1991).

The anti-predator responses of social mongooses are well-developed and coordinated, and are correlated with a number of vocalizations associated with vigilance and alarm situations. Meerkats have a sentinel system of guarding (Clutton-Brock et al. 1999b), mob certain predators as a group (Graw & Manser 2007), and coordinate group movement when responding to predators (Furrer & Manser submitted). They have distinct vocalizations used during all these activities, such as sentinel vocalizations

(Manser 1999) and a complicated, urgency-referential alarm call system (Manser 2001; Manser et al. 2001). A complex alarm repertoire is also part of the social dwarf mongoose's vocal repertoire (Beynon & Rasa 1989). These functionally referential alarm vocalizations, combined with a sentinel system of guarding, allow individuals in social foraging groups to devote their visual attention to foraging behaviour while remaining aurally alert for warning vocalizations from group members. During predator interactions, solitary species may emit vocalizations but these are either distress vocalizations (Baker 1982) or simple alarm calls (Palomares 1991). The acoustic structures of most mongooses' vocal repertoires are unknown, however, and accurate comparisons of vocal repertoires within the family Herpestidae are not yet possible.

1.4. THIS STUDY

1.4.1. The Yellow Mongoose

The focus of my thesis is the yellow mongoose, a small, diurnal herpestid that feeds primarily on invertebrate prey animals (Zumpt 1968; Lynch 1980; Avenant & Nel 1992; Taylor & Meester 1993). These activity and foraging patterns are typical of the social mongoose species (Rood 1986; Veron et al. 2004; Perez et al. 2006), yet the yellow mongoose is a solitary forager that may sometimes forage in pairs, but only rarely in groups, even in areas where food abundance allows the formation of large family groups within a given territory (Earlé 1981; Wenhold 1990; Balmforth 2004). As yellow mongooses exhibit facultative sociality in these areas, displaying visual and vocal alarm signals, alloparental care and cooperative territory defence (Earlé 1981; Wenhold & Rasa 1994; Balmforth 2004), their solitary foraging habits have been the subject of many studies (see references in Nel & Kok 1999). Yellow mongoose group sizes are not restricted by breeding patterns, as females are polyestrous and can produce a number of litters each season (Rasa et al. 1992). Food preference (Avenant & Nel 1992), microhabitat preference (Cavallini & Nel 1995) and intraspecific foraging competition (Cavallini 1993a) are also inadequate explanations of their solitary foraging patterns (Nel

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& Kok 1999). Nel and Kok (1999) postulated that phylogenetic inertia – nonadaptive phenotypic stasis (sensu Wilson 1975) – has held back the foraging group sizes of the yellow mongoose. The consequences of their phylogenetic background can undoubtedly affect their solitary behavioural patterns, as recent molecular and chromosomal evidence (Veron et al. 2004; Perez et al. 2006) suggest that the yellow mongoose should be grouped with the solitary mongooses. The socially foraging mongooses appear to have diverged from solitary ancestors in the early Pleistocene (Perez et al. 2006). It is still unclear what exactly has 'locked' the yellow mongoose into a solitary foraging mode, while the obligate social meerkat – in most ways similar to the yellow mongoose (Lynch 1980; Nel & Kok 1999) – capitalizes on abundant food by foraging socially.

1.4.2. Study Site

I studied the yellow mongoose at the Kuruman River Reserve (28°58'S, 21°49'E), an area in the Kalahari Desert, South Africa, that falls centrally within the distribution range of the yellow mongoose (Mills & Hess 1997). Vegetation at the Kuruman River Reserve is classified as Kalahari Thornveld (Low & Rebelo 1996) and is typical of the open habitat with opportunities for cover in which yellow mongooses usually occur (Mills & Hess 1997). The study area experienced hot, wet summers (October – April) and cold, dry winters (May – September), and had an annual rainfall of 252 mm during the time of this study. The dry bed of the Kuruman River ran through the reserve, cutting through grassy dunes and flat river terraces. In the riverbed were occasional dense thickets of mesquite, *Prosopis glandulosa,* an invasive North American thorn tree (Palgrave 1977) in which yellow mongooses regularly searched for prey. In the surrounding river terraces perennial grasses (*Eragrostis*, *Aristida*, *Stipagrostis* and *Schmidtia* spp) grew, and the area was dominated by low shrubs, such as driedoring, *Rhigozum trichotomum,* and blue bush, *Monechma incanum*. These perennial grasses were the dominant vegetation on dunes after rain. Common trees at the study site included black thorn, *Acacia mellifera*, grey camel thorn, *Acacia haemotoxylon* and hook thorns, *Ziziphus* spp. Predators of the yellow mongoose, such as martial eagles, *Polemaetus bellicosus*, black-backed jackals, *Canis mesomelas*, and Cape cobras, *Naja nivea*, were present on the reserve, contributing

to the death of about 55% of adult, and 28% of immature yellow mongooses (chapter four). Relatively tame steenbok, *Raphicerus campestris*, herds of eland, *Tragelaphus oryx,* pied babblers, *Turtoides bicolor,* fork-tailed drongoes, *Dicrurus adsimilis*, and livestock (sheep and cattle) grazing in certain areas allowed me to observe interaction with non-predatorial species as well. Cape ground squirrels and meerkats occurred in the area and sometimes even shared sleeping burrows with yellow mongoose families. The slender mongoose was another herpestid regularly seen at the study site.

1.4.3. Study Population

In contrast to the yellow mongoose populations that were the focus of previous behavioural studies (Earlé 1981; Wenhold 1990; Wenhold & Rasa 1994; Balmforth 2004), this is a low density study population in which natal philopatry does not occur. The nine focal groups in this population consisted of 3.7 ± 0.4 (mean $\pm$ SE) individuals sharing a territory, which is similar to group sizes for yellow mongooses elsewhere in the Kalahari (Rasa et al. 1992). The only long-term occupants of a given territory were the mated pair, and offspring (2-3 born per litter) dispersed at the age of 9-12 months to establish territories of their own. Even when the seasonal rainfall level was uncharacteristically high (December 2005 – January 2006), allowing some pairs to breed twice in quick succession, the older litters did not 'help' at the sleeping burrow and dispersed shortly before reaching adulthood. The family groups at the Kuruman River Reserve are therefore unstable, and the population structure does not resemble that of obligate social species. This population contrasts with those of Earlé (1981), Wenhold and Rasa (1994), and Balmforth (2004), which were high and medium-density populations in which territories were occupied by groups ranging between 4 and 13 members per group. The higher densities of these populations may be attributable to higher food availability – due to higher annual rainfall (Balmforth 2004) and food made available at rubbish dumps (Earlé 1981) – and territory saturation in the farmland (Balmforth 2004) and island (Earlé 1981; Wenhold 1990) habitats. Facultative sociality was evident in higher density populations, where offspring delay dispersal for some time, helping their parents raise subsequent litters and defend the territory (Earlé 1981;

Wenhold 1990; Balmforth 2004). This thesis describes the first close-range behavioural research conducted on a low-density population of yellow mongooses.

1.4.4. Study Aims

In chapter two I describe the vocal repertoire of the yellow mongoose and how this relates to its social structure. Chapter three focuses on the effect that the presence of group members has on the communicative behaviour of the yellow mongoose in a predator context. I continue my focus on anti-predator behaviour by investigating vigilance in chapter four, comparing the vigilance patterns of yellow mongooses directly with that of the sympatric obligate social meerkat to try and determine the influence of sociality on vigilance behaviour. I further investigate the influence of sociality on communicative behaviour in chapter five, by comparing the scent marking behaviour of a low density population of yellow mongooses with a high density population at a different study site (Wenhold & Rasa 1994).

I expected the vocal repertoire of the yellow mongoose to be smaller than in obligate social mongooses, as yellow mongooses do not need signals to coordinate group movement or maintain dominance hierarchies. However, I expected to find an audience effect in the yellow mongoose's alarm responses, as their alarm signals are examples of true communication, implying an awareness of their audience even though conspecifics are not frequently together while foraging. I anticipated that the yellow mongoose's foraging behaviour would be affected by their phylogenetic history and resemble those of solitary species. Lastly, in this low-density population, there are no large groups that occupy territories for extended periods of time, and therefore I predicted that their scent marking behaviour would resemble that of solitary mongooses.

CHAPTER TWO

THE VOCAL REPERTOIRE IN A SOLITARY FORAGING CARNIVORE REFLECTS FACULTATIVE SOCIALITY

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(Naturwissenschaften, under review)

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2.1. ABSTRACT

We describe the vocal repertoire of a facultatively social carnivore, the yellow mongoose, *Cynictis penicillata*. Using a combination of close-range observations, recordings, and experiments with simulated predators, we were able to obtain clear descriptions of call structure and function for a wide range of calls used by this herpestid. The vocal repertoire of the yellow mongooses comprised nine call types, half of which were used in affiliative contexts, and half in aggressive interactions. The yellow mongoose used an urgency-based alarm calling system, indicating high and low urgency through two distinct call types. Compared to solitary mongooses, the yellow mongoose has a large proportion of affiliative vocalizations, but their vocal repertoire is smaller and less context-specific than those of social species. The vocal repertoire of the yellow mongoose appears to reflect facultative sociality in this species.

2.2. INTRODUCTION

Whereas some research has indicated that social complexity can drive vocal repertoire size (McComb & Semple 2005; Freeberg 2006), this hypothesis is only tentatively supported in other taxa (Wong et al. 1999; Wilkinson 2003). In the family Herpestidae, the link between sociality and vocal repertoire is not clear, as the mainly solitary white-tailed mongoose, *Ichneumia albicauda,* for example, has a rich vocal repertoire (Mills & Hess 1997). The 36 species in this family (Nowak 1999) span the range from a solitary lifestyle, e.g. in the slender mongoose, *Herpestes sanguineus*, to obligate sociality as found in the meerkat, *Suricata suricatta.* In contrast to the larger social carnivores, in which the primary benefit of sociality is the communal hunting of prey (MacDonald 1983), the main factor promoting and maintaining sociality in mongooses is probably communal anti-predator defense, especially the protection of vulnerable young (Gorman 1979; Rood 1986). Mongooses are the only small carnivores to have formed cohesive social groups (Rood 1986), and radio-tracking studies have indicated the existence of amicable coalitions between solitary herpestids even outside the breeding season (Rood

1989; Waser et al. 1994). As such, the herpestids form an ideal group on which to focus studies on the influence of sociality on the vocal repertoire.

There have been detailed studies on the anti-predator behavior, communication and social interactions in social mongooses, such as the dwarf mongoose (Rasa 1987; Beynon & Rasa 1989; Rood 1990), banded mongoose, *Mungos mungo* (Cant 2000; de Luca & Ginsburg 2001; Müller & Manser 2007), and meerkat (Manser et al. 2001; Clutton-Brock et al. 2004; Sharpe 2005). In contrast to solitary species, such as the slender mongoose (Baker 1982; 1984) and water mongoose, *Atilax paludinosus* (Baker 1988b; a; 1998), these social species appear to have rich vocal and behavioral repertoires.

The elaborate anti-predator defenses of social mongooses include sentinel systems in the dwarf mongoose (Rasa 1989a) and meerkat (Clutton-Brock et al. 1999b), communal mobbing of predators (Apps 1992; Graw & Manser 2007), and complex alarm vocalizations (Beynon & Rasa 1989; Manser et al. 2002). Solitary species, in contrast, do not appear to have alarm vocalizations (Baker 1982; 1988b) or any defenses based on cooperation, such as communal vigilance or communal mobbing. The alarm calls of meerkats are labeled functionally referential (sensu Macedonia & Evans 1993), as they are predator-specific vocalizations that evoke specific responses from receivers, that are seen as more complex that calls that indicate risk alone. Although the complexity of alarm call repertoires has been linked to increased sociality in marmots, genus *Marmota* (Blumstein & Armitage 1997), sociality – which has limited variation within non-marmot sciurid rodent taxa – appears to have had no effect on alarm call complexity in other taxa, such as ground squirrels, genus *Spermophilus*, and prairie dogs, genus *Cynomys* (Blumstein & Armitage 1997). Other factors, such as habitat complexity, which affects the escape options that prey animals face (Macedonia & Evans 1993), and group cohesion (Furrer & Manser submitted), have, by contrast, had a strong influence on alarm call repertoires.

With a few exceptions (Earlé 1981; Palomares 1991; Wenhold & Rasa 1994), close-range behavioural studies of solitary or solitary-foraging mongooses have been conducted on animals living in captivity (e.g. Baker 1982; 1988b), whereas studies in the wild were focused on radio-tracking data and indirect behavioural measures (Cavallini 1993a; Ray 1997). In contrast, much of the behavioural data concerning obligate social

species has been obtained through close-range observations of habituated populations during long-term study projects (e.g. Rasa 1983; Clutton-Brock et al. 1998; Cant et al. 2002). Currently, direct comparisons of behavioural repertoires between social and other species are therefore hard to make. The yellow mongoose, *Cynictis penicillata*, however, has been studied in the wild by some researchers (Earlé 1981; Wenhold & Rasa 1994; Balmforth 2004), starting to bridge this gap in our knowledge.

The yellow mongoose is a small, diurnal, insectivorous herpestid that varies between solitary (Lynch 1980) and facultatively social (Earlé 1981; Rasa et al. 1992) across its distribution range. In contrast to the typically social lifestyles of other small, diurnal, insectivorous mongooses, the yellow mongoose forages alone, and has been placed in the clade of solitary mongooses (Wozencraft 1989; Veron et al. 2004). The yellow mongoose is reported to be a quiet species, with a limited number of vocalizations (Earlé 1981; Wenhold 1990) that are rarely used. We were able to record the vocal repertoire of a yellow mongoose population that was habituated to close-range observations (described in chapter three), and describe soft call types that have not been documented at other study sites. In this study population, cooperation between group members was restricted to the mated pair that mutually raises offspring, but in areas of high territory saturation offspring may help to raise subsequent litters and exhibit cooperative behaviours at the sleeping burrow that indicate facultative sociality in this species (Balmforth 2004).

Here we describe the structure of yellow mongoose vocalizations, the context in which they were used, and discuss their functions. We pay particular attention to the size of their vocal repertoire and the nature of their alarm call repertoire. We predict that the size of their vocal repertoire would be smaller than of obligate social mongoose species, as they do not need to coordinate group movement or vigilance while foraging. On the other hand, they interact regularly with conspecifics at their den, and therefore we expected yellow mongooses to have a larger variety of call types used in affiliative contexts, compared to the call types described for solitary species.

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2.3. METHODS

2.3.1. Study Site

We studied a habituated population of yellow mongooses at the Kuruman River Reserve (28°58'S, 21°49'E) in the Kalahari Desert, South Africa (for a description of the study site see Clutton-Brock et al. 1999a). Each of the nine family groups we investigated consisted of the mated pair and their most recent offspring (two to three per litter) that dispersed shortly before reaching one year of age. Individuals foraged alone for 85% of the time (chapter three), and therefore the bulk of all social interactions took place in the morning and evening at the sleeping burrows. Predators of mongooses, such as martial eagles, *Polemaetus bellicosus*, and black-backed jackals, *Canis mesomelas,* were present on the reserve and yellow mongooses shared this habitat with meerkats and slender mongooses.

2.3.2. Data Collection

Between January and December 2005 we conducted daily observations during morning and afternoon peak activity periods, collecting data on a handheld computer (Psion organizer II model LZ64). We focused on one individual per session, but described all observed social interactions and vocalizations on an *ad libitum* basis (Altman 1974), noting individuals involved, identity of dominant animals and context of vocalizations, where applicable. Vocalizations were recorded opportunistically on a Marantz portable recorder (model PMD670) connected to a directional Sennheiser (ME66/K6) microphone.

As alarm vocalizations were elicited by unpredictable events and thus rarely recorded, we performed experiments with simulated predators in order to describe alarm call structure and function more accurately. A terrestrial predator encounter was staged by walking a trained dog on a leash closer to the focal mongoose group, and a 'raptor' attack, by flying a kite (2 m x 2.5 m) painted with the image of a martial eagle at an estimated distance of 50 m (50 -70 m high) from the focal group. Reactions to the

experiments were recorded on a Marantz portable recorder (model PMD670) and a video camera (Sony HDR-HC3 4MP Handicam), both connected to Sennheiser (ME66/K6) microphones. Yellow mongoose responses in the experimental situations were similar to those observed during natural predator encounters (for a more detailed description, see chapter three). We combined *ad libitum* observations with results from simulated predator experiments, to determine if different alarm calls were associated with distinct predator types, or if they varied depending on risk.

2.3.3. Acoustic Analysis

We transferred all audio recordings to a PC using Cool Edit 2000 (Syntrillium Software Corporation, Arizona) and analyzed acoustic signals with Avisoft-SASLab Pro 4.38 software (Specht 2002), a programme also used in the analyses of other herpestid vocalizations (e.g. Manser 2001). Several call parameters (Table 2.1) were measured from call spectrograms and power spectra using a Hamming window setting, 512 point fast Fourier transformation length and 87.5 % window overlap. Calls were classified according to structure and context, and for analysis we selected only those calls with a high signal-to-noise ratio. We labeled 8 types of vocalization according to acoustic structure, distinguishing between calls primarily on the basis of bandwidth, peak frequency, and energy distribution.

Although most vocalizations were clearly distinct in acoustic structure, others were relatively similar and were primarily distinguished on the basis of the different contexts in which they occurred. Preliminary discriminant function analysis (DFA) suggested that most vocalizations were distinct, but three groups of calls closely resembled each other. For these sets of call types we tested if the *a priori* classifications into different call types were correct, using DFA. Discriminant function analyses were performed to distinguish between (1) the low growl and rolling alarm call; (2) the mobbing call, krr and recruitment vocalization; and, (3) for only one male, the mating call, mobbing call, krr and recruitment vocalization. To avoid pseudoreplication, we used a subset of calls by randomly extracting one call of each type for every individual. To perform the analysis on the mating calls, we used all the vocalizations of one specific

individual, as this was the only animal for which we recorded this type of calls. As call parameters were not distributed normally, we log transformed data before analysis (Quinn & Keough 2002). An initial DFA was performed for each group of calls, using all 10 parameters (Table 2.1), and subsequently a second DFA was conducted using only those parameters that distinguished the best between call types in the initial DFAs. The predictive power of the linear discriminant functions obtained in the second DFA was tested through leave-one-out crossvalidation, which is a conservative test of predictive ability (Quinn & Keough 2002). In this method, each case is reclassified according to the function derived from all cases other than that one (Everitt 2005).

Table 2.1. Call parameters measured for each yellow mongoose vocalization.

Parameter	Units	Explanation
Duration	seconds	time from start to end of call
Dur.ratio	none	time until maximum amplitude/ duration of entire call
Pf (start)	Hz	peak frequency at start of call
Pf (max)	Hz	peak frequency at point of maximum call amplitude
Fund (mean)	Hz	mean fundamental frequency of the call
Entr (mean)	none	average entropy of the entire call
BW	Hz	bandwidth; difference between maximum and minimum frequency of the call
L.qrt	Hz	'lower quartile,' below which point 25% of the call's energy lies
M.qrt	Hz	'medium quartile,' below which 50% of the call's energy lies
U.qrt	Hz	'upper quartile,' below which 75% of the call's energy lies

2.4. RESULTS

2.4.1. Size of the Vocal Repertoire

We distinguished eight types of yellow mongoose vocalisations according to their acoustic structure and the context they were given in. Five call types were highly distinct, whereas the other three call types were acoustically similar. According to DFA, the rolling alarm ($n = 9$) and low growl ($n = 9$) could be accurately distinguished on the basis of spectral characteristics. The cross-validated success rate of the DFA classification was

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77.8 %, compared to a success rate of 50% expected by random classification. The call parameters that explained most of the variation between these two call types were the lower quartile, medium quartile and bandwidth. The low growl had the widest bandwidth, and its energy was concentrated on a higher frequency than that of the rolling alarm.

Mobbing calls bore definite resemblance to both recruitment and krr vocalizations, according to DFA (Fig. 2.1a). The crossvalidated success rate for classification into three call types ($n = 7$ mobbing calls, 13 krr vocalizations, 13 recruitment vocalizations) was high (69.7 %) compared to chance classification (33.3 %) but this was probably due to the high distinction between recruitment and krr vocalizations. The classification success between these two call types alone was 82.0%, compared to a chance classification of 50%. The three call types were distinguished on the basis of duration, bandwidth and the lower quartile. Krr vocalizations were the longest calls, with the narrowest bandwidth; mobbing calls had a wider bandwidth and higher lower quartile than the other two call types; whereas recruitment vocalizations were the shortest calls with the lowest lower quartile of the three.

For one adult male we were able to record mating vocalizations. From these recordings we could determine that mating calls ($n = 31$) were distinct from other call types (Fig. 2.1b; cross-validated success rate = 82.0%, compared to chance expectation of 25%), and mobbing calls ($n = 10$) closely resembled krr ($n =3$) and recruitment vocalizations ($n = 6$). These four call types were distinguished on the basis of lower quartile, bandwidth and entropy. The mating call was distinct from the other call types in having a much wider bandwidth and lowest lower quartile, i.e. the energy of mating calls was concentrated in higher frequencies.
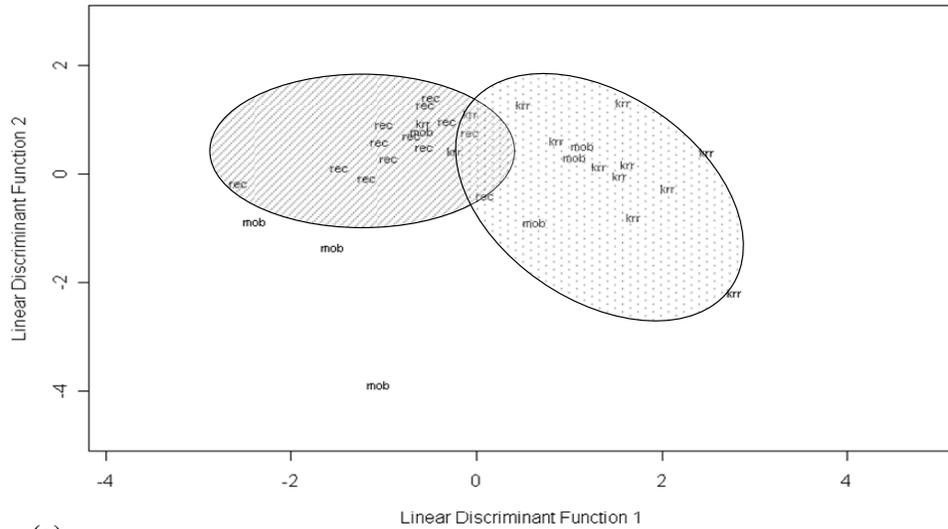
(a)
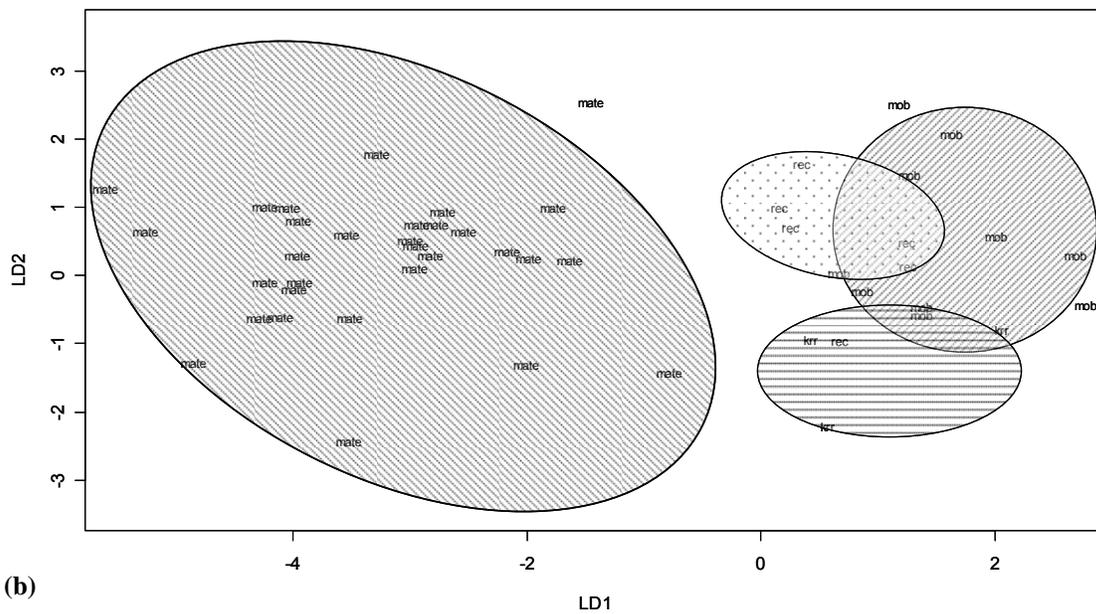
(b)

Figure 2.1. The first two linear discriminant functions (LD1 and LD2) from the discriminant function analysis of two groups of yellow mongoose vocalizations. **(a)** Distinction between recruitment ('rec'), mobbing ('mob') and krr vocalizations ('krr'). **(b)** The recruitment, mobbing, and krr vocalization for one male that uttered mating vocalizations ('mate'). This male's vocalizations were compared with one another to ascertain whether or not mating calls were distinct from the other cluster of calls.

2.4.1.1. Rolling alarm

The rolling alarm call (Fig. 2.2a) was an explosive and short vocalization (less than a second in duration) that sounded similar to a growl, at a lower pitch. Both Wenhold (1990) and Earlé (1981) described this alarm call as a 'bark,' but we can not confirm this. Only on one occasion did an alarm vocalization sound similar to a dog-like bark, and this was a peepgrowl that was uttered during an unusually high state of anxiety (see below). Rolling alarm calls were only used in the context of predator alarms ($N = 112$ events) and elicited flight and increased vigilance from conspecifics.
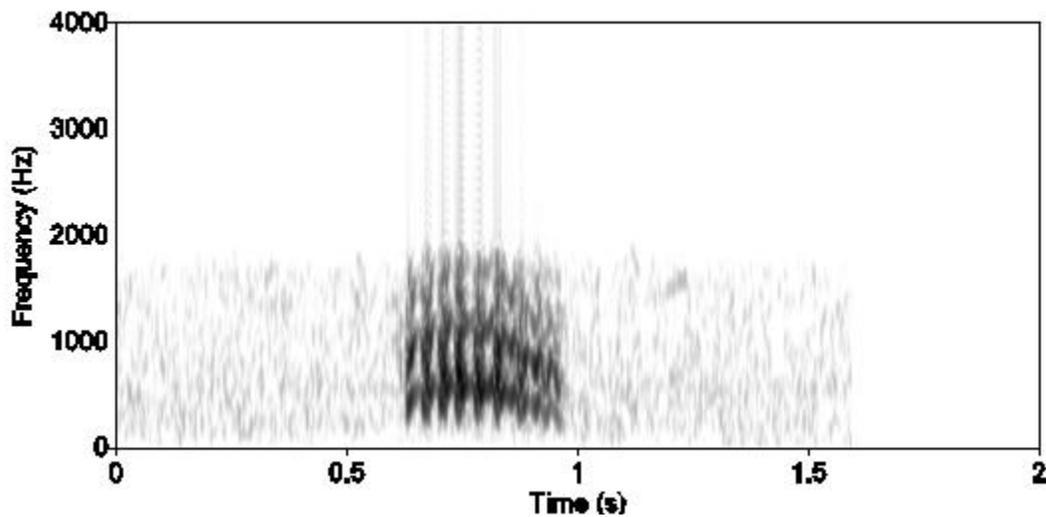
Figure 2.2a. The acoustic structure of the rolling alarm call.

2.4.1.2. Peepgrowl

The peepgrowl (Fig. 2.2b) typically consisted of a soft peeping sound immediately followed by a growl that rose in pitch towards the end of the call. On one occasion, when an adult was confronted with the anal mark of a foreign male (potential intruder) at the sleeping burrow where he was babysitting, the growl-part of this call became extremely harsh and resembled the barking of a domestic dog. Wenhold (1990) described the peepgrowl as a repeated 'warning growl' followed by a sharp 'tshack' but our acoustic analyses showed that the growl was the second part of this type of vocalization. This author did not describe this call type in social contexts other than alarm (Wenhold 1990), but we recorded it both in alarm contexts ($N = 22$ events) and during aggressive social interactions ($N = 58$ events). It was repetitive and, when there was a predator present, elicited flight in conspecifics or an increased state of alertness. During conflicts with group members, the peepgrowl appeared to be used as a threat signal, when individuals were highly agitated but not yet at the point of attacking each other.
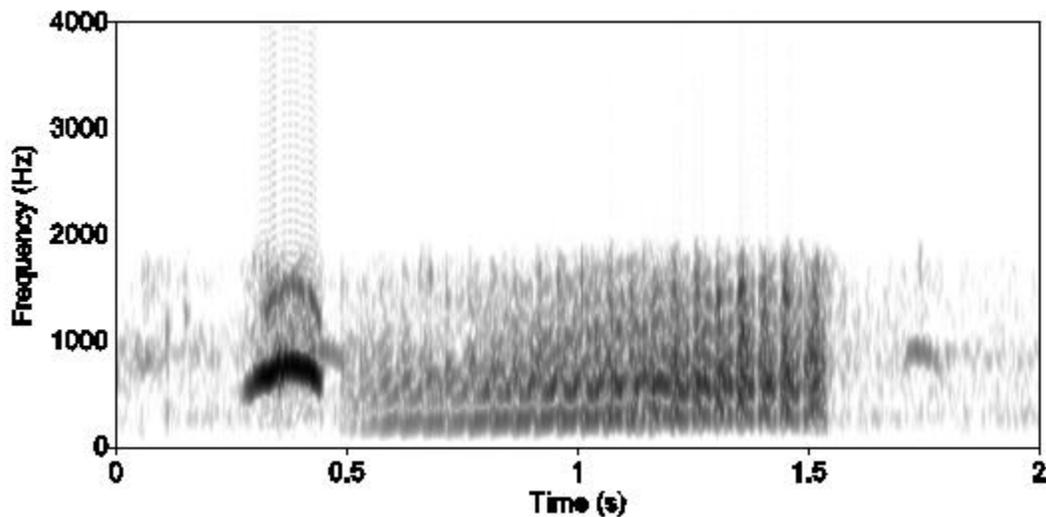
Figure 2.2b. The acoustic structure of the peepgrowl.

2.4.1.3. Low growl

The low growl (Fig. 2.2c) was a soft, low pitched, repetitive growling sound that warned conspecifics away, used mainly during intersibling food competitions (similar description in Earlé 1981). The low growl ($N = 108$ observations) appeared to carry a threat message, and was followed by attack only if the warned conspecific did not move away. During such attacks, low growls were usually interspersed with chase calls.
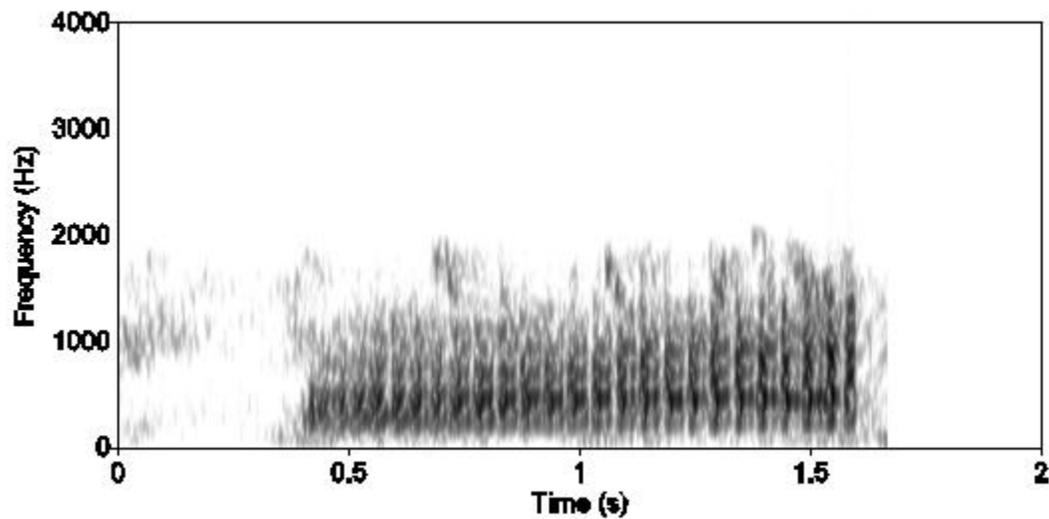
Figure 2.2c. The acoustic structure of the low growl.

2.4.1.4. Chase call

This sharp, screeching vocalization (Fig. 2.2d) was a loud, noisy call (Earlé 1981; Wenhold 1990) that occurred between group members during fights. It differed in context from the low growl in that the chase call always accompanied physical attack or aggressive chasing and biting ($N = 32$ observations). The chase call was usually uttered by the dominant individual.
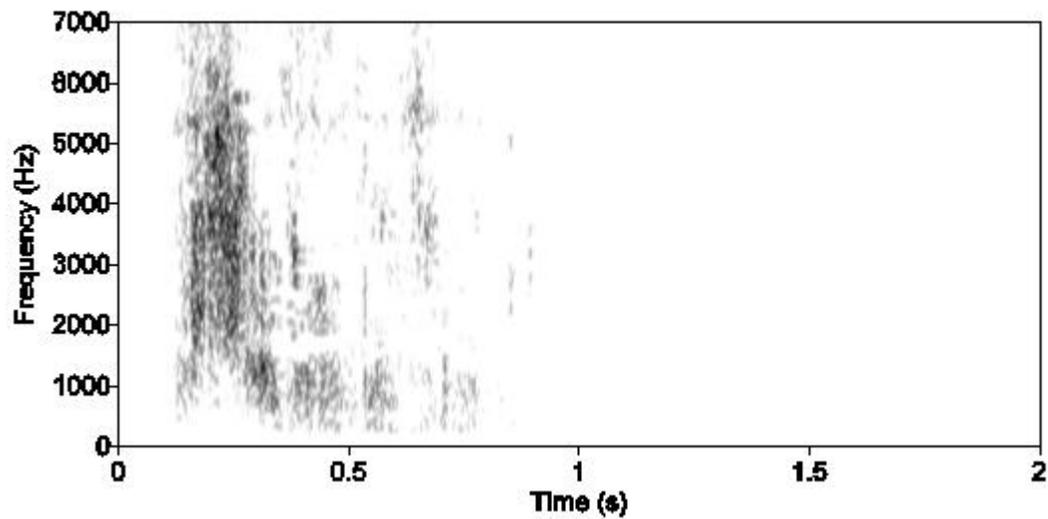
Figure 2.2d. The acoustic structure of the chase call.

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2.4.1.5. Krr vocalization

This onomatopoeic vocalization (Fig. 2.2e) was a soft, bird-like, trilling sound typically uttered by pups when accompanying adults on a foraging trip. It was probably a begging call, and pups were often very persistent in the use of this call. On more than 90% of occasions (39 out of 40 observations), however, the adults did not respond to the krr vocalization by feeding the pup, and pupfeeding happened only rarely ($N = 15$ pupfeeds noted) after pups started foraging away from the sleeping burrow, at the age of two months. The krr vocalization strongly resembled vocalizations given by adults during snake mobbing (see below).
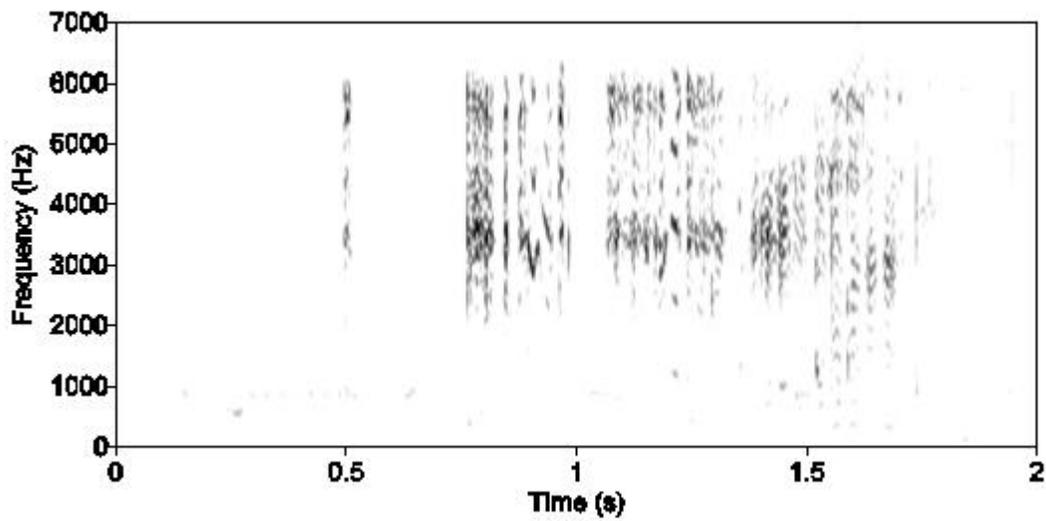
Figure 2.2e. The acoustic structure of the krr vocalization.

2.4.1.6. Mobbing call

Mobbing calls (Fig. 2.2f) sounded like a very loud, aggressive krr vocalization. These calls were recorded during snake mobbings ($N = 3$ observations) and may have been the same as vocalizations heard (but not recorded) during aggressive interspecific interactions, when yellow mongooses chased small groups of meerkats away from their sleeping burrow. It is questionable if this call is separate from the krr vocalization (see DFA results), but the amplitude and context of these calls were so distinct from those of the krr vocalization that we tentatively deem it to be a separate type of vocalization.
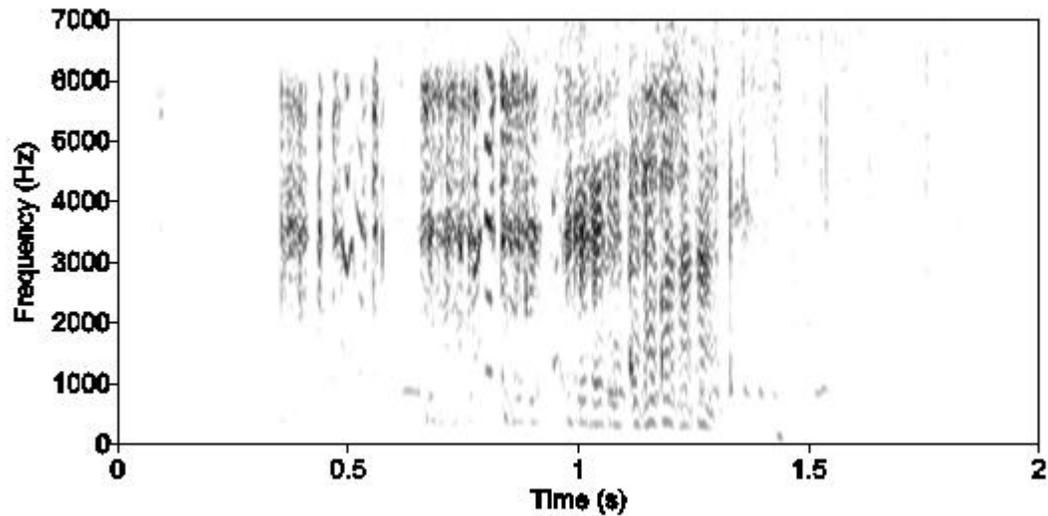
Figure 2.2f. The acoustic structure of the mobbing call.

2.4.1.7. Recruitment vocalization

These vocalizations (Fig. 2.2g) were repetitive, loud, honking calls typically used by adults returning to a sleeping burrow with large food items. After this call was uttered by the adult, pups would emerge from the burrow to be fed (more than 50 observations). A series of recruitment vocalizations was once given by an adult female during a snake mobbing, and resulted in her pups following her away from the snake, which was being mobbed by the adult male. This therefore appears to be a general recruitment vocalization that gathers group members to the caller, and is not just restricted to the pupfeeding context.
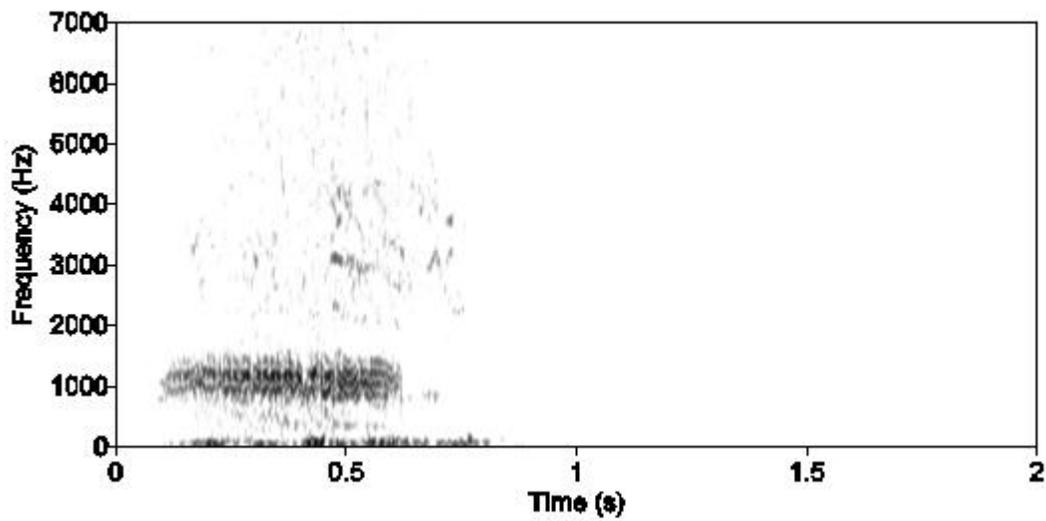
Figure 2.2g. The acoustic structure of the recruitment call

2.4.1.8. Mating call

Mating vocalizations (Fig. 2.2h) were recorded from one adult male approaching his mate during the breeding season. The mating calls were high pitched, noisy vocalizations that resembled the braying noise of a donkey. Wenhold (1990) noted a 'keening' vocalization used by males during mating, which may have been this vocalization. We noted, but did not record, similar mating calls used by two other males during this time. We did not observe mating events following these calls, only sharp rebuffs by the apparently unwilling female.
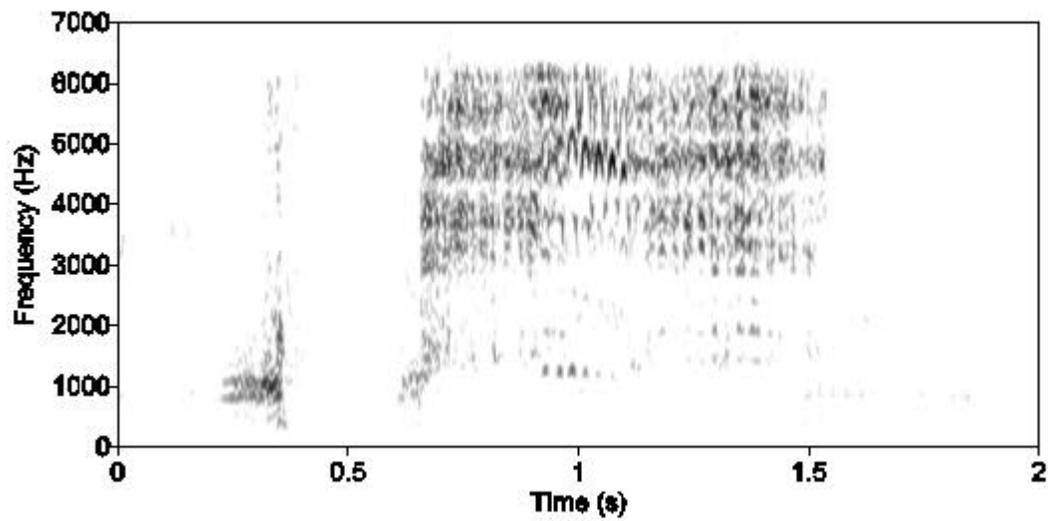
Figure 2.2h. The acoustic structure of the mating call.

2.4.2. Alarm Calls

The presence of predators did not always lead to alarm vocalizations in yellow mongooses. Although 112 rolling alarms and 22 peepgrowls were noted during natural observations, only a few could be ascribed to specific predators (Table 2.2). Combining data from natural observations with controlled experiments (Table 2.2), we showed that rolling alarm calls tended to be associated with raptor attacks (Fisher exact test: $P = 0.026$), which are high-risk predators. However, rolling alarms were occasionally used in response to terrestrial threats and in some situations mongooses used a combination of calls in a series of vocalizations ('mixed series', Table 2.2). Regardless of predator type, 72% of all rolling alarms observed were preceded by bipedal guarding (a highly alert state) and followed by instant flight below ground. In contrast, only 32% of peepgrowls were preceded by bipedal guarding, and callers usually remained above ground, repeating the call while the threat remained in view. This trend was reflected in the mixed series of calls: on two occasions, for example, a bird of prey was perched in trees near a sleeping burrow and the adult mongoose gave repeated peepgrowls, interspersed by rolling alarms and increased alertness whenever the raptor flew between perches. Calls were therefore not specifically associated with predator type, but with perceived risk.

Table 2.2. The number of events where alarm calls was elicited by identifiable predators. All 'mixed' series of calls (call series consisting of both types of alarm call) were uttered while the caller was close to a bolthole and the predator remained nearby.

Data source	Call type	Aerial	Terrestrial
Natural observations	Rolling alarm	8	3
	Peepgrowl	0	2
	Mixed series	2	2
Experiment	Rolling alarm	4	3
	Peepgrowl	0	3
	Mixed series	1	2
All data combined	Rolling alarm	12	6
	Peepgrowl	0	5
	Mixed series	3	4

2.5. DISCUSSION

Yellow mongooses have a repertoire of at least eight vocalizations which are used in multiple contexts. A ninth reported vocalization – a purring sound that accompanies mating (Earlé 1981; Wenhold 1990) – adds to this repertoire, but mating events were never observed in this study. Three of the yellow mongoose's vocalizations – the peepgrowl, low growl, and chase call – were used during intraspecific conflict situations, such as foraging competitions and dominance interactions. A fourth aggressive vocalization, the mobbing call, was used during interspecific conflicts in which the yellow mongoose actively tried to chase the other species away. All of these calls appeared to convey a threatening or warning message and few of these interactions ever escalated to serious fights. This suggests that yellow mongooses use communicative signals to mediate conflict, similar to other species living in groups (Moynihan 1998). Threat vocalizations such as these, are a feature of most herpestids' vocal repertoires, whether they are social or solitary species (Kingdon 1997).

In contrast to other solitary foraging mongooses, more than half the calls in the yellow mongoose's vocal repertoire – the rolling alarm, krr vocalization, recruitment

vocalization, mating call and possible mating purr – were used only in affiliative contexts. These vocalizations were used to warn kin of danger, during biparental care of offspring, or as part of their mating ritual. In contrast, only two of the seven vocalizations noted for the solitary foraging Egyptian mongoose – the alarm and 'contact call' – were employed in nonaggressive contexts (Palomares 1991). The solitary slender mongoose, similarly, uses most of its vocalizations under agonistic circumstances (Baker 1982). As a high proportion of affiliative vocalizations in a species' repertoire could be an indicator of increased sociality (Schassburger 1993), this aspect of the yellow mongoose's vocal repertoire may be linked to its facultatively social nature.

The yellow mongoose does not need to coordinate vigilance or group movement while foraging, and therefore lacks a number of vocalizations that are typical of socially foraging mongooses (e.g. Manser 1998; Furrer & Manser submitted). All the social mongoose species, and also the Egyptian mongoose –an occasional group forager (Palomares 1991) – have contact calls in their repertoires (Kingdon 1997). These calls are used to maintain group cohesion and inter-individual spacing (e.g. in meerkats: Manser 1998), similar to the contact calls of many group-living species (Cheney et al. 1996; Tyack 2003; Cortopassi & Bradbury 2006). Other calls that are absent from the yellow mongoose's vocal repertoire include the 'sentinel calls' that meerkats use to announce vigilance during sentinel duty (Manser 1999), and the 'lead calls' that adult meerkats use to encourage other group members to follow them on a foraging trip (Manser 1998). Compared to social herpestids, the yellow mongoose's vocal repertoire is smaller and less diverse, mainly due to its solitary habits away from the sleeping burrow.

The yellow mongoose's vocal repertoire, and specifically the alarm call repertoire, is less context specific than those of social species. The yellow mongoose indicates high and low risk through different call types, namely the rolling alarm and peepgrowl, respectively. In other species a simple urgency-based alarm call repertoire has been attributed to their living in a two-dimensional habitat (Macedonia & Evans 1993) or linked to a low degree of sociality (marmots: Blumstein & Armitage 1997). Two social mongooses, meerkats (Manser 2001) and dwarf mongooses (Beynon & Rasa 1989), live in open habitats and exhibit complex, functionally referential alarm calling. As the yellow mongoose lives in a similar habitat yet differs from these species in terms of sociality,

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their simple alarm call repertoire appears to be linked to their low level of sociality, rather than habitat complexity. However, the distinction between yellow mongoose and meerkat alarm calls can still be attributed to differential escape options, as affected by cooperation between group members. Whereas yellow mongooses hold their heads in a horizontal, alert position while foraging, individual meerkats keep their heads down while foraging (chapter four) and rely on vocalizations from group members to warn them of danger (Manser et al. 2001). Yellow mongooses do not usually need to interrupt foraging to visually verify the nature of a threat, and therefore a simple alarm calling system offers sufficient warning of danger. Meerkats, on the other hand, rely heavily on the accuracy of the auditory information they receive, as responses to predator alarms can interrupt foraging time substantially (Manser et al. 2001). Incorrect flight responses are very costly to meerkats in terms of foraging time and even more in getting separated from the rest of the group (Furrer & Manser submitted), and the advantages of an functionally referential alarm call repertoire are potentially great. Communal anti-predator vigilance – a hallmark of sociality in meerkats – has thus affected meerkat foraging habits and escape options, and thereby led to a more complex alarm calling system in this species. Due to yellow mongooses' alert foraging habits, a simple, non-specific alarm call repertoire is sufficient.

Yellow mongooses' facultatively social nature (Balmforth 2004) appears to be reflected in their vocal repertoire, which is more complex than those of solitary species, but smaller and less context-specific than those of highly social species. In contrast to primarily solitary mongooses, yellow mongooses have a number of vocalizations used in affiliative contexts, and communication in this species is not focused solely on mediating aggressive interactions. The vocal repertoire exhibited in this low density population of yellow mongooses suggests that individuals have the potential to respond flexibly to additional social pressures if ecological factors were to favour natal philopatry (as found by: Balmforth 2004; Earlé 1981; Wenhold 1990). Although the yellow mongoose is a quiet species, it shows a level of vocal sophistication that supports previous findings that it lies in between the solitary and social mongooses in terms of sociality and cooperation (Earlé 1981; Balmforth 2004).

CHAPTER THREE

THE AUDIENCE EFFECT IN A FACULTATIVELY SOCIAL MAMMAL, THE YELLOW MONGOOSE, *CYNICTIS PENICILLATA*

(A. le Roux, M. I. Cherry, M. B. Manser)

(Animal Behaviour, in press)

3.1. ABSTRACT

The audience effect has been demonstrated in numerous group-living vertebrates but whether it is present in facultatively social species is unknown. We investigated the anti-predator responses of the yellow mongoose, a mammal that dens in groups, but primarily forages alone. To examine the effect that the social environment has on their communication, we performed a combination of field observations and experiments with live and model predators on a habituated population of mongooses. Social context affected both the communicative and flight behaviour of yellow mongooses. Alarm vocalizations were used almost exclusively when individuals were in a group, rather than solitary. The visual alarm signal – a raised tail – was predominantly used by solitary individuals, when predators were outside attack range. This study is the first to show an audience effect in a facultatively social mammal, suggesting that even rare social interactions lead to the ability to respond flexibly to predators depending on the presence or absence of conspecifics.

3.2. INTRODUCTION

Research has highlighted the almost ubiquitous nature of the audience effect amongst social vertebrates, present in species ranging from chickens, *Gallus domesticus* (Marler et al. 1986), and zebra finches, *Taeniopygia guttata* (Vignal et al. 2004), to brown capuchin monkeys, *Cebus apella* (Pollick et al. 2005) and Siamese fighting fish, *Betta splendens* (Doutrelant et al. 2001). This effect is where signal production appears to be under voluntary control by the signaller, specifically mediated by the social environment of the sender, and not only by the original stimulus (such as the presence of a predator or food). The audience effect has been shown in the signaling behaviour of many social species, yet it has never been investigated in species that are not obligate social. It is not known if the signaling behaviour of such species would be affected by the limited number of intraspecific encounters that they experience.

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The audience effect, if present in facultatively social species, should be especially evident in their anti-predator responses. Individual prey actions, including inappropriate signaling during predator encounters, have potentially fatal costs to the actor, and in group-living species predator alarms are often strongly affected by the nature of the conspecific audience (e.g. Hoogland 1983; Hauber & Sherman 1998). Predation exerts strong pressure on grouping behaviour (e.g. Barta et al. 2004) and alarm signals are a well-studied aspect of most gregarious species' vocal repertoires (review in Klump & Shalter 1984). Solitary species, in contrast, may use distress calls during predator encounters or stressful situations (Baker 1988; Mascagni & Doyle 1993), but these signals are reflexive vocalizations affected by the presence of the threat alone (Marler 1967). As obligate social species respond flexibly to social context in terms of behaviour, the study of facultatively social species could shed light on the effects of increasing gregariousness on the solitary ancestors of social species.

Ancestors of the mongooses – family Herpestidae – have been suggested to be solitary, and sociality to have evolved only once in this group (Veron et al. 2004; Perez et al. 2006). The family shows the full range of social structures, from solitary to facultative and obligate group-living, with the obligate social species in a monophyletic clade that is separate from the clade that includes the solitary and facultatively social species (Veron et al. 2004; Perez et al. 2006). Alarm signaling behaviour is absent in the vocal repertoire of solitary herpestids, such as slender mongooses, *Herpestes sanguineus* (Baker 1982), and water mongooses, *Atilax paludinosus* (Baker 1988), which have only distress vocalizations. Obligate social mongooses, in contrast, have complex alarm calling repertoires (dwarf mongooses, *Helogale undulata*: Beynon & Rasa 1989; meerkats, *Suricata suricatta*: Manser 2001) and are affected by the presence of a conspecific audience (Rasmussen 2006). Yellow mongooses are solitary foragers that belong to the solitary herpestid clade (Veron et al. 2004) and have both a visual and vocal alarm signal (Earlé 1981; Balmforth 2004). Although they den alone in some parts of their distribution range (Cavallini 1993), yellow mongooses share sleeping burrows and territories with family members elsewhere, where they display facultative sociality and cooperation (Earlé 1981; Balmforth 2004). Unlike obligate social and solitary species, the yellow mongoose forages alone but encounters closely-related conspecifics on a regular basis.

This constantly fluctuating social environment makes it an ideal candidate for the investigation of the audience effect.

We habituated and closely followed individuals in a wild population of yellow mongooses, allowing us to compare their behaviours in a social as well as solitary context without manipulating their natural social circumstances. All individuals in this population, both immature and adult, foraged alone most of their time but occasionally foraged with one or two family members. We used a combination of data from observations and experiments to test the prediction that alarm signals are mediated by the social environment of the sender, specifically by the presence or absence of a conspecific audience.

3.3. METHODS

3.3.1. Study Site and Population

We studied a population of yellow mongooses at the Kuruman River Reserve (28°58'S, 21°49'E) in the Kalahari Desert, South Africa. The study area experienced hot, wet summers (October – April) and cold, dry winters (May – September), and consisted of the dry bed of the Kuruman River and the surrounding dune areas (see Clutton-Brock et al. 1998, 1999 for detailed description). Predators of the yellow mongoose, such as martial eagles, *Polemaetus bellicosus*, black-backed jackals, *Canis mesomelas*, and Cape cobras, *Naja nivea*, were present on the reserve. During the study period from February 2004 to March 2006, 55% of the adults (older than one year of age) and 28% of the immature (younger than one year of age) yellow mongooses were predated by either raptors or canids (A. le Roux, unpublished data). The average size of groups denning together was 3.7 ± 0.4 (mean $\pm$ SE) for our nine focal groups, each consisting of the mated pair with their most recent offspring. Offspring dispersed before reaching adulthood and no helpers remained behind to help raise the next year's litter, so that the only long-term group members were the mated pair. This was a low density population of

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yellow mongooses, with group sizes similar to those reported for other populations in the Kalahari ($n = 4$-5 members, Rasa et al. 1992).

3.3.2. Field Observations

We achieved habituation of 21 individuals (10 males, 11 females) through daily visits to sleeping burrows, initially sitting quietly 30 m away, in full view of unhabituated animals, gradually starting to move and walk around slowly as habituation progressed. Movements or indirect approaches were only attempted when the unhabituated animal was visibly relaxed and undisturbed by the presence of a still observer, and movements were stopped whenever animals became too nervous. While we were with focal animals we would regularly hum softly, as a 'reassurance' call that mongooses may associate with the presence of 'harmless' observers. Eventually, these individuals were habituated to the close presence of a human observer and their natural behaviour was not disturbed by our presence, so that we could walk with them, remaining as close as 5 m from a normally foraging mongoose. To keep track of group movements we fitted one adult per group ($N = 9$) with a radio collar from Sirtrack$^{©}$ (Havelock North, New Zealand), whereas other group members were identified through small dye-marks on their fur. Each individual was implanted with an Identipet™ (Johannesburg, South Africa) microchip transponder. Although only a few individuals were radio collared, we were able to locate all focal animals with ease, as each animal shared a sleeping burrow with one radio collared adult.

We conducted daily observations between January and December 2005 during morning and afternoon peak activity periods. Before each session we chose a focal animal from the 21 habituated individuals and followed it as it left the sleeping burrow in the morning, or located and followed individuals in the afternoon. Thus, between two observers, we had four different mongooses as focal animals each day. Although all visible animals in the surrounding area were monitored, our focus was always on one individual per session, as groups rarely stayed together while foraging. The area was carefully scanned at least once every five mins to check for the proximity of other individuals. Whereas animals mostly foraged alone, we were able to collect data for each focal animal while solitary and while in a family group.

We collected data *ad libitum* (Altman 1974) on a handheld computer (Psion organiser II model LZ64), defining the following behavioural categories: (1) guarding behaviour, and (2) alarm responses. Guarding was the cessation of all other activities for more than one second in order to scan the area, a 'bipedal guard' being exhibited when a vigilant mongoose stood on its hind legs. Alarm responses occurred when high threat levels were perceived and were associated with flight reactions. We distinguished between two non-vocal flight responses and two types of vocal alarm calls. Non-vocal alarm responses were either fleeing without any alarm display, or flight in conjunction with the pilo-erected, raised tail. As this 'tail signal' was occasionally seen during other social interactions it was classified as a visual alarm only when clearly associated with fleeing from a predator. Vocal alarms were either the 'rolling' alarm, or the 'peepgrowl.' These vocalizations could be differentiated by ear on the basis of acoustic structure (chapter two). The peepgrowl was also observed in non-alarm situations and was interpreted as an alarm call only if followed by flight behaviour and/ or bipedal guarding.

3.3.3. Experiments with Simulated Predation Threat

Over 400 predator sightings were recorded during field observations (mainly of raptors, at a distance of more than 100 m away), but the primary anti-predator reactions of yellow mongooses were alert, silent guarding bouts. Most of the alarm responses during over 900 h of observation were to threats unseen by the observer, and we seldom saw interactions with natural predators in close proximity. In order to describe more detailed reactions to predators at a closer distance, we conducted a series of experiments with simulated predators, namely a model of a martial eagle, a medium-sized live dog, and a live Cape cobra. We presented each of these predators to solitary yellow mongooses ($N = 7$ kite trials, 6 dog trials, 6 snake trials) as well as groups ($N = 8$ kite trials, 8 dog trials, 4 snake trials). Only adults (age: older than one year, $N = 8$) were focal animals during experiments, and we were able to use most individuals ($N = 5$) in both a solitary and group context. As habituation levels varied between individuals and some adults died before the end of our study, we were unable to perform experiments on all nine family groups. Experiments were spaced with at least a week between trials at the same group

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and we conducted trials of different stimuli types in a random order. We did not include non-predatorial species in our experiments, as mongooses' responses to these species were commonly seen during field observations. We regularly observed mongooses reacting to species such as steenbok, *Raphicerus campestris,* eland, *Tragelaphus oryx,* and yellow-billed hornbills, *Tockus flavirostris,* and the primary reaction was to ignore them or guard briefly, even if the other species were closer than 10 m (in the case of tame eland).

Staged raptor encounters took the form of a kite (2 m x 2.5 m) painted with the image of a martial eagle, flown at an estimated distance of 50 m (50 -70 m high) from the focal animal or group. We repeated these trials in two cases where focal animals failed to spot the 'raptor' in the initial experiment. In trials imitating an encounter with a terrestrial predator, an assistant walked a trained dog on a leash towards the focal yellow mongoose at a constant walking speed. To induce mobbing behaviour we presented yellow mongooses with a live Cape cobra in a clear, aerated Plexiglas box (dimensions 70 x 70 x 80 cm) and showed this box without the snake to six individuals to control for its possible influence. We conducted half of the control trials before any snake presentations, and half after presentation sessions, separated by at least a week. In all experiments we video recorded responses of focal animals on a Camcorder (Sony HDR-HC3 4MP Handicam) connected to a directional Sennheiser (ME66/K6) microphone. Recordings were analysed for both behaviour and type of vocalization used (chapter two).

3.3.4. Statistical Analyses

All statistical analyses were conducted in the freeware program R for Microsoft Windows version 2.3.1 (R Core Development Team 2006). To determine if an equal number of predators were noticed by mongooses in different social contexts, we compared the observed number of guarding bouts (in which a predator was also identified by the observer) with the expected number of guarding bouts, using unequal variance *t*-tests of the ranked data (Ruxton 2006). To generate the expected number of guarding bouts, we assumed that the chance for a mongoose to encounter a predator while solitary would be proportional to the amount of time spent alone. Because focal animals were solitary for

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85% of the time, we predicted that 85% of individuals' guarding bouts would occur while they were solitary, and 15%, while in a group.

We analysed the likelihood of displaying an alarm signal, depending on the presence or absence of an audience, with binomial generalized linear mixed-effect models, using a penalized quasi-likelihood approach (the *glmmPQL* function in the 'MASS' package of R 2.3.1 (Venables & Ripley 2002)). For these analyses we focused on all instances where an alarm response (with or without signaling) was shown during field observations, and coded the binomial response variable as 0 = no signal, versus 1 = signal, discounting of the number of alarm signals given at that instant. We did not include calling rate as a variable in our analyses as the main vocal alarm used (the rolling alarm) was always singular, and data on calling rates for the repetitive peepgrowl were too limited. We ran separate models for vocal and visual signals, as there was no *a priori* reason to assume that these signals were directed at the same receiver, whether the predator or conspecifics. The mixed-effect model allowed us to incorporate individual identity as a random factor; and predator type and social context as fixed factors affecting the likelihood of calling. Predator type was coded into three categories: unknown (invisible to the observer), terrestrial, and aerial. Although all these threats evoked an alarm response of some kind, the latter two predator classes were deemed as most threatening, as predators that we could not see were presumably far away (yet evidently visible to the mongoose). We simplified maximal mixed-effect models to obtain the minimum adequate model by systematically removing interactions where *P*-values were higher than 0.01 and main effects with *P*-values higher than 0.05 (Crawley 2005). We present only the results of significant effects here.

In statistical analyses of experimental data we combined the results from the raptor and dog experiments, as we were interested in the reaction to perceived threat as mediated by the conspecific audience, rather than specific predator types. The likelihood of calling was not affected by predator type (see results of glmmPQL analyses). We did not include snake mobbing in statistical analyses, as this was recorded only five times during natural observations and we could not reliably induce this behaviour in our experiments.

3.3.5. Ethical Note

Radio collars and transponders were fitted during live-captures in which individuals were anaesthetized using the cyclohexamine drug Zoletil (average dose 0.10mg/ kg). Box traps baited with meat scraps were set at known, active sleeping burrows, checked every 20 min while open, and captured animals were immediately transferred to cloth bags which reduced handling time and simplified injections. Zoletil was injected intramuscularly and average induction time was two min. Morphological measurements, collaring and DNA sampling were done while animals were fully anaesthetized. Recovery started ten min later and individuals were under constant supervision in an aerated, shaded recovery box until reflexes were deemed to be normal (after 2 – 3 h). Captured animals were returned to their sleeping burrows and closely monitored over the following days for any signs of discomfort or changes in behaviour. There were no observed negative after-effects due to the drug, nor did trapping methods dehabituate individuals – we frequently found the same animals returning to traps, sometimes repeatedly on the same day. This protocol appears to be highly effective for a solitary foraging species in which removal from a social group does not cause undue disturbance. Collars never exceeded 4% of the mongoose's bodyweight (18 ± 1.1 g collars, with an average body weight of 640.7 ± 22.6 g for collar bearers) and recaptures to replace old collars did not reveal abrasions due to tight collar fitting.

For snake experiments a Cape cobra was captured by an experienced snake handler and it was kept in an aerated terrarium with free access to water for less than 3 weeks. The cobra was released unharmed in the territory where it had been found. We conducted all observations, experiments and captures with permission from the Northern Cape Department of Nature Conservation and the University of Stellenbosch's ethical committee.

3.4. RESULTS

The number of predators eliciting guarding behaviour from yellow mongooses was similar to expected values for solitary individuals (17.3 ± 3.8 bouts per individual, unequal variance t-test: $t_{31.63} = -0.12$, $P = 0.91$) and those in a group (2.6 ± 0.8 bouts per individual, $t_{29.46} = -1.17$, $P = 0.25$). Observers did not notice any predators that were unseen by yellow mongooses, in either social context. While solitary, adult and immature mongooses gave a similar proportion of alarm calls (Table 3.1; binomial test of proportions: $\chi^2_1 = 0.08$, $P = 0.78$), and tail signals (Table 3.1; $\chi^2_1 = 0.60$, $P = 0.44$).

Vocal alarm signals were unaffected by the type of predator encountered ($P > 0.05$) but individuals in a group were more likely to call than those on their own (fig 3.1a; glmmPQL: $t_{126} = 7.03$, $P < 0.001$; odds ratio (OR) = 40.08). The tail signal, by contrast, was affected by predator type as well as the presence of an audience. In the presence of group members (fig 3.1a; $t_{125} = -5.41$, $P < 0.001$; OR = 0.09) yellow mongooses displayed fewer tail signals than when solitary. In the presence of a predator visible to the observer ($t_{125} = -2.12$, $P = 0.035$; OR = 0.57) individuals were less likely to display than when in the presence of a visible predator. Specifically, there was no difference in signaling behaviour between terrestrial and aerial predators ($P > 0.05$) but terrestrial predators elicited fewer tail displays than did unseen threats ($t_{125} = -2.13$, $P = 0.035$).

Table 3.1. The number of alarm signals given by individual yellow mongooses while foraging solitary or in a group.
* adult individuals (older than one year)

Individual identity	Vocal alarm		Visual alarm	
	Solitary	Group	Solitary	Group
bf02	0	1	0	0
bf04	0	0	1	0
cf05	0	0	5	1
cm01 *	0	4	7	0
cm02 *	2	0	4	0
cm03 *	0	0	8	0
df03	1	4	0	0
df04	0	3	0	0
ff04	1	0	5	1
gm01 *	0	1	3	0
hm02	0	1	0	0
jf03	0	1	0	0
tf02 *	0	16	0	0
tf08	0	1	1	1
tm02 *	0	12	4	2
tm06	0	1	1	1
zf06	0	0	1	1
zm01 *	2	11	10	4
zm05	0	1	0	0
TOTAL	6	57	50	11

Yellow mongooses' responses to the kite and domestic dog experiments were similar to reactions observed during natural predator encounters. Both solitary individuals and mongooses in a group fled to the nearest bolthole in response to the simulated raptor, occasionally vocalizing (Fig. 3.1b). In response to the dog, solitary yellow individuals ran away past nearby refuges, remaining aboveground while stopping infrequently to keep visual track of the approaching predator. When a group of mongooses encountered the dog, individuals ran to the nearest bolthole but emerged again within less than a minute to

monitor the dog's movements. The focal animal in a group would occasionally stay above ground at the mouth of a burrow entrance and allow the dog to come as close as 2 m before going below ground. Solitary individuals never vocalized in response to either of these predators, whereas the majority of group experiments induced acoustic alarms (Fig. 3.1b). The experimental results support the prediction that the presence of conspecifics has a significant, positive influence on the likelihood of vocalizing (binomial test of proportions: $\chi^2_1 = 16.0$, $P < 0.001$). Tail signals were more likely to be displayed during solitary than social trails ($\chi^2_1 = 3.42$, $P = 0.07$).
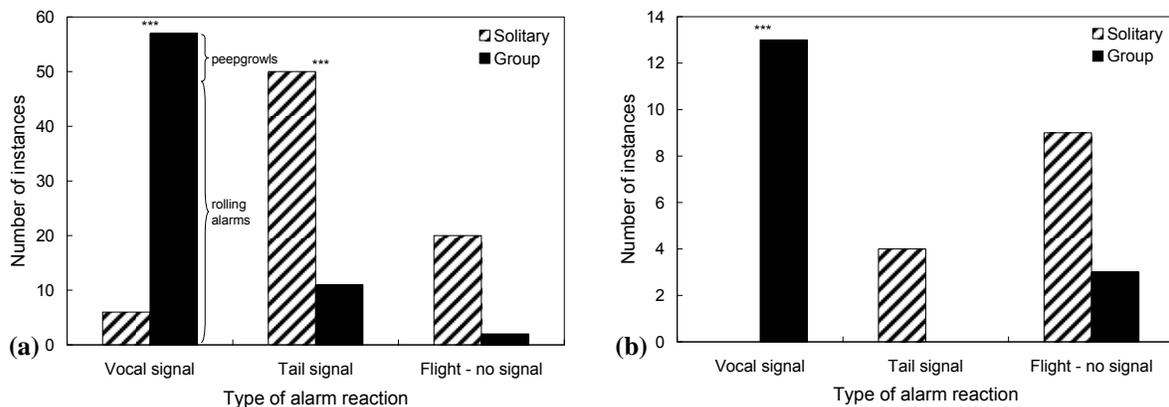
Figure 3.1. Occurrences of alarm signals during **(a)** field observations of yellow mongooses and **(b)** experiments with simulated terrestrial (dog) and aerial (kite) predators. Experiment: eight vocal alarms in response to dog; five to kite; one tail signal in response to dog, and three, to kite experiment. (*** *P* < 0.001).

Five natural snake mobbings were recorded during field observations. Two of these were mobbing groups and the other three were solitary mobbings. Typical mobbing behaviour, whether of a Cape cobra or puff adder, *Bitis arietans*, consisted of the solitary mongoose (or group) repeatedly approaching and spit-calling at the snake, with pilo-erected fur and puffed-up tail. Spit-calls were non-harmonic, harsh sounds uttered when an individual came within 1 m of the snake, lunging at it as if to bite. While mobbing, the agitated mongoose would energetically renovate nearby boltholes and anal mark the area,

and sometimes utter 'krr'-vocalizations (chapter two). These high-pitched, trilling, bird-like calls, were only used by mobbers in a group ($N = 2$ instances).

Mobbing behaviour during experiments was the same as naturally observed snake mobbings, described above. Mobbing did not occur during every experiment ($N = 6$ solitary, $N = 4$ group experiments), as only two of the four groups, and none of the solitary individuals mobbed the Cape cobra. The focal animal uttered krr-vocalizations in one of these two mobbing events. Control experiments ($N = 6$) with the empty box never elicited mobbing behaviour and the box was largely ignored. This differed from the reactions of yellow mongooses to the predator, as the box was actively avoided when containing a snake, even though mobbing did not occur in eight of the ten experiments. In both natural and experimental snake mobbings the only observable difference between solitary and group mobbing was the absence of krr-vocalizations in solitary mobbings.

3.5. DISCUSSION

The alarm signals and anti-predator behaviour of the yellow mongoose were not merely an involuntary response to the presence of predators, but were affected by social context. As individuals live in family groups, the yellow mongoose's vocal alarm is probably an experience independent behaviour that functions to warn close kin of impending danger, similar to other alarm-calling species (Maynard Smith 1965; Dunford 1977; Griesser & Ekman 2004). In many social species, the accuracy of alarm calling and responses matures over time through learning and/ or a developmental process of maturation (Seyfarth & Cheney 1986; Ramakrishnan & Coss 2000; Hollén & Manser 2006). Immature yellow mongooses called 'correctly' – in a group as opposed to solitary context – as often as adults, suggesting that responses were accurate early on in their ontological development. They may be 'fast learners' but we consider this to be improbable. Mongoose pups spend the first two months of their lives at the sleeping burrow in the presence of group members and may have learned from conspecifics to use alarm vocalizations when predators are in sight, but it is unlikely that learning was involved in the appropriate suppression of calls. Most predators eliciting an alarm response were at

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too great a distance to locate yellow mongooses on the basis of their alarm vocalizations, which were inaudible to observers further than 10 m away (pers. obs.). Learning is enhanced through a high cost to incorrect behaviours (Dukas 1998), and in the absence of such costs, yellow mongooses have little incentive to learn the suppression of alarm calling behaviour while alone. At this stage, therefore, we cannot attribute correct call production to maturation or learning. However, yellow mongoose groups responded more nervously than solitary individuals to alarm situations. Groups responded to terrestrial predators by fleeing to a nearby bolthole, instead of evading capture while remaining above ground, as solitary individuals did. Yellow mongooses are also more flighty and vigilant in groups than when alone (chapter four) even though they encounter equivalent numbers of predators. Vocalizing may therefore reflect the caller's motivational state rather than implying intentional communication to conspecifics (Cheney & Seyfarth 1985; Hauser 1997).

The tail signal was elicited under opposite circumstances to the vocal alarm, when neither predators nor conspecifics were nearby. Unlike alarm vocalizations, the visual alarm was a very conspicuous signal unlikely to be missed by visually hunting predators such as raptors (Tucker 2000) and diurnal canids (Wells & Bekoff 1982). This signal may therefore have been directed at the predator (Hasson 1991). Attacking predators may be thwarted by having their attention redirected to a conspicuous, non-vulnerable part of the body, such as a distinct tail tip (Humphries & Driver 1970; Powell 1982), or be startled by sudden, bright coloration (Humphries & Driver 1970). However, yellow mongooses did not display the visual alarm signal when predators were nearby and about to attack. Communicating with a distant predator, the tail signal probably advertised perception and thereby deterred pursuit (Woodland et al. 1980; Murphy 2007). Similar to numerous prey species (Cott 1940), the yellow mongoose forages close to cover, using camouflage as a protective measure (chapter four). The presence of one or two conspecifics increases the visibility of an individual, which may be why they do not increase their vulnerability even further by displaying the tail signal when in a group. The tail signal does appear to increase vigilance in conspecifics (Balmforth 2004), and we suggest that the visual alarm of the yellow mongoose is a long distance signal with both the predator and conspecifics as potential receivers.

Communication during snake mobbing events also showed an audience effect. Although few mobbing events were observed, solitary mongooses mobbed snakes without using the krr-vocalization, as opposed to groups, which did vocalize. This call type is not an alarm signal (chapter two), but may function as a recruitment call bringing group members together during interspecific conflict situations. Unlike the harsh spit-call, which is presumably directed at the snake, the krr-vocalization is a signal directed at group members, and is used only in a gregarious context. Again, the selective use of a communicative signal showed the effect that the presence or absence of group members had on signallers.

To our knowledge, this study is the first to explicitly demonstrate an audience effect in a solitary foraging species. In two social species with occasionally solitary males – Thomas langurs, *Presbytis thomasi* (Wich & Sterck 2003), and meerkats (Rasmussen 2006) – these solitary males exhibit an audience effect in their vocalizations. However, these are gregarious species in which social awareness is expected to have evolved. The meerkat, for example, is daily engaged in communal activities and complex, cooperative anti-predator behaviours (Clutton-Brock et al. 2001; Manser et al. 2002) that could lead to the development of cognitive skills similar to those of other social species (Whiten & Byrne 1997; Bond et al. 2003). In contrast, the yellow mongoose is at best facultatively social in areas where ecological pressures force them to den – but not forage – in more permanent groups (Balmforth 2004).

Some solitary and solitary-foraging carnivores show behavioural patterns that resemble those usually ascribed to social species. The social behaviours and physiology of the solitary wolverine, *Gulo gulo*, are affected by social circumstances in ways similar to those of gregarious species (Dalerum et al. 2006). Slender mongooses, a solitary species, may form long-lasting male-male coalitions (Rood 1989; Waser et al. 1994). Yellow mongooses, which primarily forage alone across their distribution range and exhibit vigilance patterns adapted to a solitary foraging lifestyle (chapter four), respond flexibly to predators in the presence of conspecifics. The social behaviours of solitary and solitary-foraging species may therefore be more adaptable than hitherto acknowledged, and flexible responses to conspecifics are probably not limited to social species. Future studies of social cognition and communication should include species that are not

obligate social, as their limited intraspecific interactions may have led to a more plastic behavioural repertoire than previously appreciated.

CHAPTER FOUR

VIGILANCE BEHAVIOUR AND FITNESS CONSEQUENCES COMPARED BETWEEN A SOLITARY AND A GROUP FORAGING MAMMAL

(A. le Roux, M. I. Cherry, M. B. Manser)

Chris who?

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4.1. ABSTRACT

Vigilance behaviour in gregarious species has been studied extensively, especially the relationship between individual vigilance and foraging 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 anti-predator tactics. We investigated predator avoidance behaviour in the yellow mongoose, *Cynictis penicillata*, a solitary foraging carnivore, and compared it with a sympatric, socially foraging congener, the meerkat, *Suricata suricatta*. The presence of conspecifics reduced foraging time and success of yellow mongooses and increased individual vigilance, contrary to the classical group-size effect. Sociality did not affect overt vigilance, but influenced general patterns of predator avoidance. Whereas meerkats relied on communal vigilance and auditory warnings against danger, yellow mongooses avoided predator detection by remaining close to cover and increasing low cost vigilance that did not interfere with other activities such as foraging. Survival rates of yellow mongooses and meerkats were similar, and survival rates for the adults of both species were lower than those of their young. We suggest that foraging group size in herpestids is not only constrained by ecological factors such as food distribution, but also by species-distinct vigilance patterns.

4.2. INTRODUCTION

Animals across all vertebrate taxa forage in social groups, and the causes and consequences of aggregation have been studied intensively (Elgar 1989; Lima & Dill 1990; Beauchamp 2003). Predation risk is often cited as a primary factor in maintaining grouping behaviour (Bekoff et al. 1984; Ebensperger & Blumstein 2006). Individuals foraging in larger groups benefit from a greater number of alert conspecifics that are likely to detect predators before an attack, and a greater number of prey individuals makes it less likely that a specific individual will be predated during a successful attack (Elgar 1989; Quenette 1990; Bednekoff & Lima 1998). There is a tendency for individual

vigilance to decline with an increase in foraging group size, allowing individuals more foraging time (Quenette 1990). These anti-predator benefits outweigh the costs of having to be vigilant against potential food competitors: in the majority of studies on non-primate species individuals show a group-size effect, having lower vigilance levels in large groups than in small groups (Lima 1995; Beauchamp 2003).

Predation risk affects the time budget and microhabitat use of prey animals whether or not individuals are foraging in a group. Under higher risk of predation, individuals may decrease general activity levels, forage at different times of the day, change their manner and rate of food harvesting, or restrict movements to safer areas of their microhabitat (Kotler 1984; Tchabovsky et al. 2001a). Subtle changes in movement patterns, such as intermittent locomotion, are employed to improve the ability of prey to detect threats (McAdam & Kramer 1998), and may reduce their visibility to predators (Kramer & McLaughlin 2001). Responses to predators are generally affected by individual vulnerability and risk perception, irrespective of group size (Childress & Lung 2003). Young animals, especially, are highly vulnerable to predation due to small body size and the need to still acquire adult-like anti-predator responses (Galef 1976; Boinski 1987).

As Beauchamp (2003) pointed out, the causes of changes in vigilance, and the expected pattern of changes due to group size and sociality are still unclear. Some interspecific studies have tried to address the relative importance of environmental, social and morphological factors on the wariness of gregarious and solitary animals. Blumstein (2006) found that body size explains the evolution of flightiness in bird species, and cooperative breeders tend to be more nervous than non-cooperative species. The sociality of closely related species of gerbellid rodent did not affect individual vigilance, although intraspecific variation in sociality did (Tchabovsky et al. 2001b). With interspecific studies of vigilance, confounding factors such as habitat type and differential diets (Kaby & Lind 2003; Manaf et al. 2003) often make it difficult to isolate the effect of sociality itself. Vigilance is also a harder concept to define than previously thought, as birds, for example, can still detect potential attacks while foraging in a 'non-vigilant' state (Lima & Bednekoff 1999). Many questions thus remain concerning the interaction of social,

predation and environmental effects on vigilance in prey animals – and the majority of studies have focused on vigilance only in social foragers (Treves 2000).

We studied anti-predator tactics in a solitary foraging carnivore, the yellow mongoose, *Cynictis penicillata,* and compared it to the sympatric, group foraging meerkat*, Suricata suricatta*. The yellow mongoose dens together with kin in groups ranging from 2 to 13 members (Rasa et al. 1992) but forages mostly alone – occasionally in pairs (Nel & Kok 1999). This small, diurnal species has a vocal and visual alarm signal (Earlé 1981), but the occurrence of coordinated vigilance while foraging seems unlikely due to their solitary foraging habits. Their diet, habitat and predator suite overlap strongly with that of the obligate social meerkat (Lynch 1980), which lives and forages in groups ranging from 3 to 50 members (Clutton-Brock et al. 2002) and exhibits a range of cooperative behaviours from communal rearing and anti-predator responses to teaching (Clutton-Brock et al. 2001a; Manser 2001; Manser et al. 2001; Thornton & McAuliffe 2006). During foraging meerkats often have a sentinel watching out for predators (Clutton-Brock et al. 1999b; Manser 2001), and they have evolved a sophisticated alarm call system (Clutton-Brock et al. 1999b; Manser 2001). The distinction between the two species' foraging group sizes has been ascribed to differences in intraspecific foraging competition (Cavallini 1993b), diet and microhabitat use (Avenant & Nel 1992; Rasa, cited by Nel & Kok 1999). However, none of these explanations adequately accounted for the interspecific difference in foraging behaviour (Nel & Kok 1999). Thus far, no-one has investigated possible differences in vigilance behaviour.

The aim of this study was to examine how ecological and social factors affect vigilance behaviour during foraging in the relatively solitary yellow mongoose, and compare it with the obligately social meerkat. 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) individual risk perception, such as the effect predators' presence and individual age; and c) social environment, the presence of conspecifics leading to a decrease in individual vigilance, and consequently increased foraging time and success. For social meerkats we predicted that: d) 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: e) meerkats would devote less time to vigilance than yellow mongooses, and would therefore have more time for foraging, as well as higher foraging success; f) they would differ in terms of microhabitat use, yellow mongooses staying closer to cover and safe refuges to counteract their lack of coordinated vigilance; and (g) the cooperative meerkats would have higher survival rates than yellow mongooses.

4.3. 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). During the study period from February 2004 to March 2006 the average group size for yellow mongooses was 3.7 ± 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. Foraging 'groups' consisted of one individual for 85% of active foraging time (see also chapter three), and varied between two and three individuals when individuals foraged in a group (15% of active foraging time). The six focal meerkat groups consisted of an average of 11.0 ± 0.8 members (ranging from $8 - 18$). Meerkat group members denned together and foraged together, so that group size did not vary in the same way as yellow mongoose group sizes. A variety of antelope, songbirds, and predators of mongoose, such as martial eagles, *Polemaetus bellicosus*, black-backed jackals, *Canis mesomelas* and Cape cobras, *Naja nivea*, were present on the reserve.

4.3.1. Observations

We achieved habituation of 21 yellow mongooses (10 males, 11 females) through daily visits to sleeping burrows, and were able to follow individuals at a distance of less than 5 m without disrupting their natural foraging behaviour (for more detail, see chapter three). We conducted daily observations from January 2005 onwards during morning and

afternoon foraging periods, collecting ad lib, 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. Ad lib data was continuously collected throughout the day, with scan data taken every five minutes, and spatial location noted every 10 minutes. These sessions were not interrupted during predator alerts. Focal observation sessions, lasting 20 minutes each, were conducted only if no predator had been spotted for at least 30 minutes beforehand, and were discontinued whenever there was a predator alarm or if the focal animal was unseen for more than 5 s. Data were collected for all individuals as soon as they started foraging around the age of 2 months. Age classes were defined as pup (0 – 3 months old), juvenile (3 – 6 months), subadult (6 to 12 months) and adult (older than 1 year). Subordinate adult meerkats in groups without foraging pups were used in focal and scan observations, based on the yellow mongoose protocol.

We performed a total of 900 h of observations on yellow mongooses, collecting 17 ± 1 days of ad lib and scan data for each solitary yellow mongoose ($N = 21$) and 8 ± 1 days for each of 18 mongooses in foraging groups. We performed 6 ± 1 focal observations on 17 solitary individuals, and 2 ± 0 focal observations each on 14 individuals in foraging groups. We conducted one morning session of scan and focal data collection for each meerkat, collecting 36 h of data for 12 meerkats (six males and six females from six groups).

Data collection focused, firstly, on wariness, categorized as either 'active' or 'passive' vigilance. Active vigilance, measured during ad lib and focal observations, was exhibited whenever a focal animal interrupted 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 one second. 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 (filmed on a Sony HDR-HC3 4MP Handicam). The most extreme anti-predator reaction was the alarm response, defined as fleeing from a threat, usually accompanied by a vocal or visual

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alarm signal. 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. In addition, for meerkats, we noted when there was a sentinel on guard (Clutton-Brock et al. 1999b).

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. 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, labeled as 'foraging pauses.'

We described the social and ecological environment by noting proximity to vegetative cover, boltholes and group members, number of group members and habitat type. Proximity to cover, in increasing order of safety, was categorized 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. Habitat was defined as either: on a dune; in the flats between dunes; or in the dry riverbed; and we further described the microhabitat according to the predominant type of vegetation, be it annuals, grass, shrubs, trees, or vegetation-free.

4.3.2. Life History

In order to see 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 and if an individual 'disappeared' while still too young to disperse (younger than nine months) we presumed it dead. As the fate of most dispersing yellow mongooses was unknown, these individuals were excluded from

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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.

4.3.3. Statistics

4.3.3.1. Vigilance

All statistical analyses were done using in R for Microsoft Windows version 2.3.1 (R Development Core Team 2006). Yellow mongoose data were obtained according to a crossover design, as each individual was observed in multiple combinations of circumstances (p 296 in Quinn & Keough 2002). This allowed us to analyse both focal and scan data using mixed-effect models with individual identity as random variable and the relevant explanatory factors as ordered, fixed effects (Pinheiro & Bates 2000). Specifically, for focal data we used linear mixed-effect models to investigate the effect of proximity to boltholes, presence and guarding behaviour of group members, habitat type, age of focal individual, and time of day on the duration of vigilance. We adjusted duration and counts to account for the proportion of time spent in proximity to a bolthole. We analysed scan data by means of generalized linear mixed-effect models with multivariate random effects, using a penalized quasi-likelihood approach (the *glmmPQL* function in R 2.3.1). These binomial models focused on the effect of distance to bolthole, presence and guarding behaviour of group members, habitat type, proximity to cover, age and time of day on the likelihood of the focal animal having a vigilant head position. We simplified maximal mixed-effect models to obtain the minimum adequate model 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. We presented results from ANOVAs of the significant main effects and/ or interactions. Cohen's effect sizes were calculated from simplified formulae in Quinn & Keough (p191, 2002) and Thalmeier & Cook (2002), where appropriate. As per convention, a 'small' effect size is suggested by a Cohen's D

value between 0.20 and 0.49; a 'medium' effect, by one between 0.50 and 0.79; whereas a D higher than 0.80 indicates a 'large' effect size (Cohen 1992). In mixed-effect models, odds ratios were calculated as a measure of effect size.

To investigate the influence of individual risk perception, we determined the duration of active vigilance in the five minutes following an initial response to a visible predator, seen by the focal animal as well as the observer. These responses could either be a guarding bout (danger level = intermediate) or alarm flight (danger level = high). Active vigilance after these anti-predator responses was compared directly with baseline levels of vigilance as determined during 20-minute focals, using Kruskal Wallis (KW) Anovas. We also counted and compared the frequency of sessions in which pups, juveniles, subadults and adults were foraging in groups to see if there were differences in grouping behaviour depending on age class.

For meerkats, we analysed the effect of the ecological and social environment on vigilance with mixed-effect models similar to those used on the yellow mongoose data. In addition to the fixed effects as used in yellow mongoose models, we incorporated the presence of a sentinel, distance to nearest and furthest group members, number of visible group members, and number of conspecifics within 5 m of the focal animal at every scan instance.

For each yellow mongoose and meerkat we obtained the average number and duration of vigilance bouts across all focal observations. Using scan observations we calculated the average proportion of observations in which head position was down, horizontal or up. For focal data we corrected measures of active vigilance for time spent within 2 m of a bolthole, as yellow mongooses remained within 2 m of a bolthole for $18.8 \pm 3.1\%$ of the focal observational time, and meerkats for $7.0 \pm 3.0\%$. We compared active and passive vigilance between solitary yellow mongooses, yellow mongoose foraging groups and meerkats by performing KW Anovas. Post-hoc tests for significant differences were Mann-Whitney U tests with Bonnferoni corrections.

4.3.3.2. Foraging behaviour

The same fixed effects as mentioned above were incorporated in linear mixed-effect models describing foraging behaviour in both yellow mongooses and meerkats. Separate models were obtained for all fixed effects on duration of foraging, foraging success and number of foraging pauses. We then compared the average durations, foraging successes and foraging pauses measured during focal observations between the two species using KW Anovas.

4.3.3.3. 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 protective cover and boltholes. We used ArcView GIS's Animal Movements extension (Hooge et al. 1999) to obtain average speed of movement for each adult yellow mongoose and focal meerkat. We compared distance to cover and boltholes, and speed between the species using KW Anovas and Mann-Whitney U tests.

4.4. RESULTS

4.4.1. Vigilance

In yellow mongooses active vigilance was only affected 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 4.1). The presence of group members, time of day, season, age of focal animal, and habitat type did not affect active vigilance (linear mixed-effect model: all P-values > 0.05). Passive vigilance was not affected by season, time of day or habitat type (glmmPQL: all P-values > 0.05). Two fixed factors were associated with heightened passive vigilance,

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namely increased proximity to cover, and increase in age (Table 4.2). Additionally, the interaction between certain factors affected vigilance (Table 4.2). To explain these interactions, we examined a detailed breakdown of the model output (a summary of which is presented here). Whereas bolthole distance and number of group members had no direct influence on vigilance (factors were non-significant on their own), these factors had an important mediating effect on vigilance behaviour. In contrast to solitary foragers, foraging groups tended to remain closer to boltholes and showed high vigilance levels, with the highest alertness found in pairs of yellow mongooses within 2 m of a bolthole, out in the open. Away from vegetative cover, vigilance increased with age but under cover, vigilance decreased sharply with age. Older individuals tended to stay closer to cover than young ones, and accordingly showed consistently lower levels of vigilance when cover and age were taken into consideration. Pups tended to remain close to boltholes, however, with correspondingly high vigilance levels.

Table 4.1. Significant effects from a linear mixed-effect model investigating active vigilance in yellow mongooses. Only the fixed factor 'bolthole' (less than 2 m from focal animal) had an influence on vigilance, and is presented here. Degrees of freedom for the denominator = 307.

Measure		*F*	*P*	Odds Ratio
bipedal guard	(duration)	7.97	0.0051	1.68×10^{11}
quadrupedal guard	(duration)	27.99	<0.0001	1.28×10^{15}
resting guard	(duration)	22.22	<0.0001	6.78×10^{30}
brief pauses	(count)	5.38	0.021	86.04
all guarding bouts	(duration)	27.65	<0.0001	4.49×10^{57}

Table 4.2. Significant effects of various fixed factors on passive vigilance in the yellow mongoose. Non-significant factors are not presented. 'cover': proximity to vegetative cover, 'bolthole': distance to nearest bolthole, 'yno': number of group members present.

Fixed factor	Df	t [a]	P	Odds Ratio
cover	408	3.01	0.003	2.25
bolthole	408	1.33	0.186	0.90
yno	408	0.77	0.445	1.08
age	5038	5.25	< 0.001	2.08
cover:age	5038	-4.46	< 0.001	0.68
bolthole:yno	408	2.72	0.007	1.24
bolthole:age [b]	5038	-2.36	0.018	0.90

[a] Positive t-values indicate an increased probability for head position to be vigilant as the factor (putative safety) increases.

[b] When the marginally significant interaction of boltholes and age was removed from the model, other significant results remain so.

Individual risk perception affected grouping behaviour and active vigilance in yellow mongooses. There was a tendency for younger mongooses to forage in groups more often than adults (Pearson's correlation: $t_2 = -6.08$, $P = 0.03$), as pups encountered group members in 77.8% of their ad lib sessions, juveniles, 55.6%, subadults, 23.5% and adults 17.0% of their sessions. Adults increased active vigilance directly after detecting or fleeing from a predator (Fig. 4.1, KW Anova: $x^2_2 = 23.07$, $P < 0.001$). This was due to bipedal guard durations being longer than baseline levels when danger levels were high ($x^2_2 = 6.54$, $P = 0.038$; post hoc tests: $P < 0.05$), and resting guard durations being longer than baseline levels when danger levels were intermediate ($x^2_2 = 13.41$, $P = 0.001$; post hoc tests: $P < 0.05$). Quadrupedal vigilance was not affected by the sighting of a predator ($x^2_2 = 4.55$, $P = 0.10$).
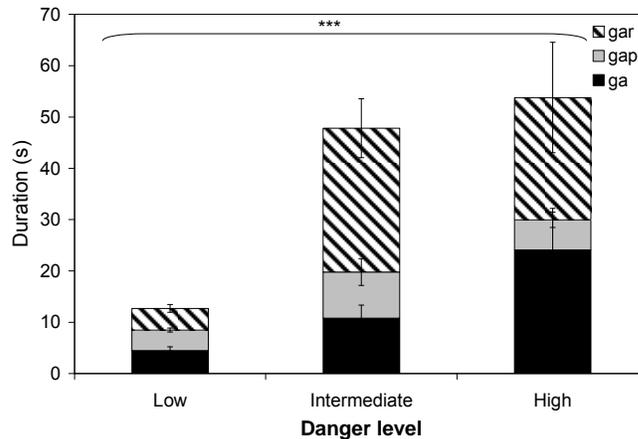
Figure 4.1. The influence of a predator sighting on the active vigilance levels of adult yellow mongooses. 'low': baseline levels of danger, no predator in sight, 'intermediate': predator sighted by mongoose, only elicited guarding reaction, 'high': predator sighted, eliciting initial flight and/ or alarm vocalization, 'gar': resting guard, 'gap': quadrupedal guard, 'ga': bipedal guard (*** $P < 0.001$)

Active vigilance in meerkats was affected by the proximity of boltholes and certain social factors, whereas passive vigilance was affected only by proximity to safety. Closer to boltholes individual vigilance duration increased, whereas the number of brief pauses decreased (Table 4.3). As the number of group members in close proximity rose, brief pauses also increased closer to boltholes. When other group members were on bipedal guard, individual bipedal guarding duration tended to decrease. However, with a higher number of individuals in close proximity, focal animals increased bipedal guarding duration, if these group members were on bipedal guard. Passive vigilance was slightly affected by distance to bolthole and proximity to cover but not by any social factors such as number of meerkats on guard or proximity to group members. Increased proximity to cover was associated with somewhat decreased vigilance (glmmPQL: $t_{76} = -1.97$, $P = 0.05$; Odds ratio (OR) = 0.62) whereas the opposite happened as individuals came closer to boltholes ($t_{76} = 2.08$, $P = 0.04$; OR = 1.28).

Table 4.3. Significant effects of fixed factors on active vigilance in meerkats, from mixed-effect models. 'bolthole': distance to nearest bolthole, 'yga': other group members on guard, 'yno': number of group members present.

Measure		factor (fixed effect)	$denDF^a$	F	P	Odds ratio
all guarding bouts	**(duration)**	bolthole	56	64.11	< 0.001	< 0.001
bipedal guard	**(duration)**	bolthole	53	31.67	< 0.001	9.21×10^{27}
bipedal guard	**(duration)**	yga	53	3.93	0.053	< 0.001
bipedal guard	**(duration)**	yno	53	2.41	0.127	0.03
bipedal guard	**(duration)**	yga: yno	53	16.68	< 0.001	7.72×10^{16}
quadrupedal guard	**(duration)**	bolthole	56	16.18	< 0.001	2.94×10^{12}
brief pauses	**(count)**	bolthole	54	12.65	< 0.001	0.06
brief pauses	**(count)**	yno	54	0.16	0.789	0.56
brief pauses	**(count)**	bolthole: yno	54	8.24	0.006	11.6

[a] Degrees of freedom for the denominator

The duration of active vigilance was equal between the two species, but they differed in type of vigilance behaviour. Yellow mongooses and meerkats spent an equal amount of time vigilant (Fig. 4.2a, two-tailed t test: $t_{21.2} = -0.976$, $P = 0.34$, Cohen's $D = 0.59$). Although quadrupedal vigilance ($t_{21.3} = -3.56$, $P = 0.002$, $D = 0.80$) and resting guard ($t_{29} = -6.03$, $P < 0.001$, $D = 1.15$) durations were much longer in yellow mongooses than meerkats, bipedal guards tended to be more frequent in meerkats ($t_{18.6} = 1.78$, $P = 0.09$, $D = 0.37$) and were equal in duration ($t_{17.3} = 0.588$, $P = 0.56$, $D = 0.26$) between the species. Yellow mongooses had significantly more guarding bouts in total than did meerkats (Fig. 4.2b, $t_{22.1} = -3.74$, $P = 0.001$, $D = 0.82$). Fifty percent of these bouts were brief pauses and the interspecific distinction can be attributed to a difference in number of brief pauses ($t_{20.9} = -4.13$, $P < 0.001$, $D = 0.87$), quadrupedal guards ($t_{19.2} = -3.39$, $P = 0.003$, $D = 0.97$) and resting guards ($t_{29} = -5.62$, $P < 0.001$, $D = 1.52$). In yellow mongoose groups, individuals directed their gazes towards group members in 62 out of 644 guarding bouts. Meerkats looked at group members in 10 out of 200 guarding bouts, paying less visual attention to conspecifics than did yellow mongooses (binomial test of proportions: $X^2_1 = 3.62$, $P = 0.06$).

Comparing the two species, yellow mongooses had a vigilant head position more often, whereas meerkats were more often surrounded by overtly vigilant group members and interrupted their foraging time more frequently for alarm responses. Meerkats spent a larger proportion of their time looking down than yellow mongooses did (Fig. 4.2c, KW Anova: $x^2{}_2 = 10.78$, $P = 0.005$, $D = 0.73$), whereas yellow mongooses spent more time with their heads held in a horizontal position (Fig. 4.2c, KW Anova: $x^2{}_2 = 10.40$, $P = 0.006$, $D = 0.78$). Post hoc tests indicated that the group and solitary values for mongooses were similar, and both were significantly different from meerkat head positions (P-values < 0.05). Both species looked up less than 3% of the observational time (Fig. 4.2c, KW Anova: $x^2{}_2 = 0.68$, $P = 0.70$, $D = 0.50$). The proportion of times that other group members were on guard was much higher for meerkats than yellow mongooses (Table 4.4, binomial test of proportions: $x^2{}_1 = 357$, $P < 0.001$). Yellow mongooses interrupted foraging for alarm responses far less than meerkats (Table 4.4, $x^2{}_1 = 30.3$, $P < 0.001$), which was mirrored in focal observations, where six out of the twelve meerkat sessions were interrupted by alarm responses, compared to one out of 149 focal sessions for yellow mongooses.

(a)

(b)

(c)
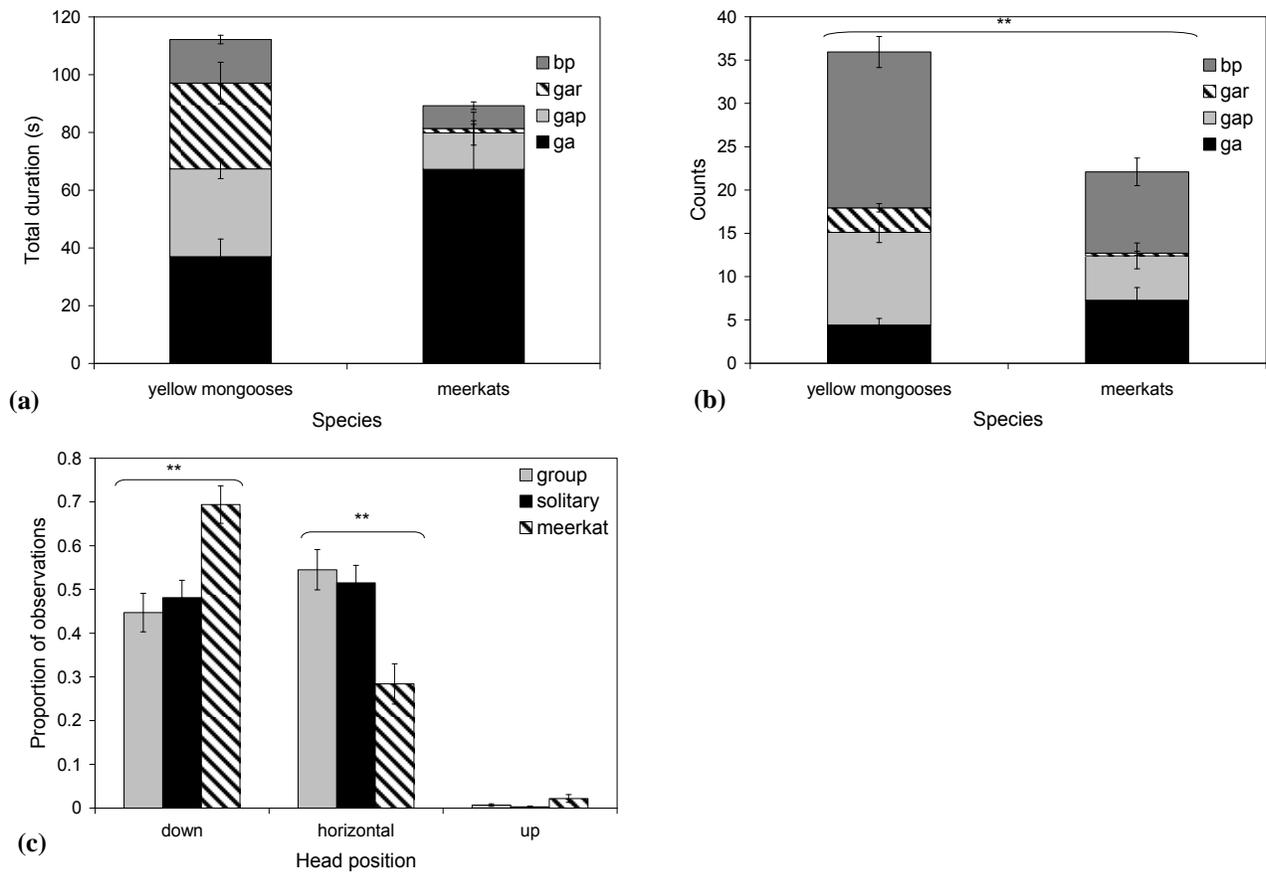
Figure 4.2: a) Duration (mean $\pm$ SE) and **b)** number of active vigilance bouts per 20 minute focal compared between yellow mongooses and meerkats. 'bp': brief pauses, 'gar': resting guard, 'gap': quadrupedal guard, 'ga': bipedal guard. Yellow mongoose group and solitary data were combined as there 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) (** $P < 0.01$)

Table 4.4. The number of scan observations on foraging groups of yellow mongooses and meerkats

Description	Yellow mongoose	Meerkat
Other individuals on guard	1	119
Interruptions due to alarm	4	17
Total number of observations	1072	380

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4.4.2. Foraging Behaviour

Fine-scale analyses of each species' foraging behaviour indicated that yellow mongooses had their highest foraging success when solitary, whereas meerkats' foraging success increased when they were surrounded by more alert conspecifics. According to mixed-effect models, neither age, season, habitat type, nor time of day had any influence on foraging bout duration, foraging success or foraging pauses of yellow mongooses (all P-values > 0.05). The number of foraging pauses was affected only by proximity to boltholes, being higher near boltholes than away from them ($F_{307} = 27.52$, $P < 0.001$, OR $= 7.58$ x 10^{15}). Solitary individuals foraged longer than those in a group (ANOVA: $F_{307} = 11.49$, $P < 0.001$, OR $= 1.41$ x 10^{47}), and also had a higher foraging success ($F_{307} = 11.39$, $P < 0.001$, OR $= 512.9$). Foraging behaviour in meerkats was affected only by social factors, with an increase in foraging bout duration when other group members were on bipedal guard ($F_{56} = 4.41$, $P = 0.04$, OR < 0.001), and a tendency for increased foraging success under the same circumstances ($F_{56} = 3.35$, $P = 0.07$, OR $= 0.03$). A higher number of individuals within 5 m of the focal animal led to a decrease in number of foraging pauses ($F_{56} = 3.24$, $P = 0.08$, OR $= 0.78$).

Comparing the species using average values for each individual, we found that solitary yellow mongooses, yellow mongoose groups and meerkats did not differ in terms of foraging behaviour or success. Yellow mongooses (solitary: 15.55 ± 2.38 s, group: 10.81 ± 1.41 s) tended to forage for shorter periods than meerkats (duration: 22.36 ± 8.24 s, KW Anova: $X^2_2 = 5.63$, $P = 0.06$, $D = 0.17$). Foraging success was similar between yellow mongooses (solitary: 12.63 ± 1.34, group: 11.52 ± 2.23) and meerkats (9.62 ± 1.62, KW Anova: $X^2_2 = 2.15$, $P = 0.34$, $D = 0.39$), as was the number of foraging pauses per focal observation session (solitary: 0.57 ± 0.09, group: 0.74 ± 0.20, meerkats: 1.25 ± 0.85, KW Anova: $X^2_2 = 0.60$, $P = 0.74$, $D = 0.36$).

4.4.3. Microhabitat Use

The two species differed in their microhabitat use while foraging, 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. 4.3a, KW Anova: $x^2{}_2 = 10.73$, $P = 0.005$, $D = 0.45$) but equal time close to cover (Fig. 4.3a, $x^2{}_2 = 2.13$, $P = 0.35$, $D = 0.39$) and in the open ($x^2{}_2 = 0.37$, $P = 0.83$, $D = 0.33$). Yellow mongooses were more often within 2 m of a bolthole (Fig. 4.3b, $x^2{}_2 = 5.99$, $P = 0.05$, $D = 0.30$), but spent less time than meerkats between 5 and 10 m from boltholes (Fig. 4.3b, $x^2{}_2 = 11.49$, $P = 0.003$, $D = 0.65$). For both these categories, distinctions were due to differences between yellow mongoose groups and meerkats (post-hoc tests: $P < 0.05$). Additionally, solitary yellow mongooses spent less time than meerkats between 5 and 10 m away from boltholes ($P < 0.05$). Yellow mongooses moved faster (0.13 ± 0.01m/s) than meerkats (0.08 ± 0.01 m/s, two-tailed t test: $t_{16.0} = -4.95$, $P < 0.001$).
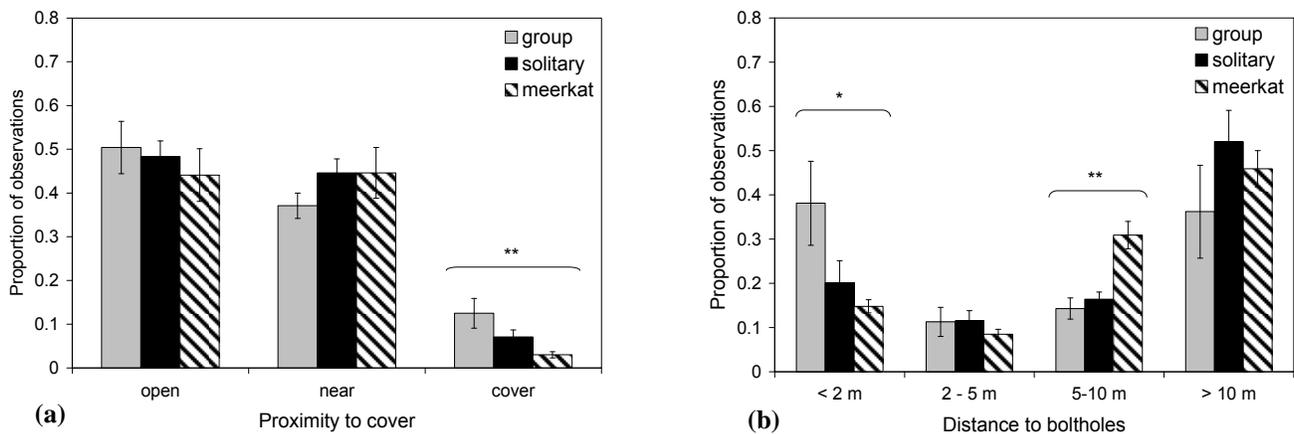

Figure 4.3. Microhabitat characteristics (mean proportion $\pm$ SE) compared between yellow mongoose groups, solitary yellow mongooses and meerkat groups (* $P = 0.05$, ** $P < 0.01$). a) Proximity to vegetative cover ('open:' more than a body length away from cover; 'near:' within a body length from cover; 'cover:' completely under cover); **b)** Proximity to boltholes.

4.4.4. Life History

There was a large interspecific difference in the absolute numbers of adults monitored and pups born during our study period (Fig. 4.4a), but the proportion of surviving individuals was similar for both species (Fig. 4.4b). Comparing yellow mongooses with meerkats, survival rates of individuals younger than six months (Fig. 4.4b, binomial test of proportions: $x^2_1 = 0.80$, $P = 0.37$), between six months and one year ($x^2_1 = 0.08$, $P = 0.78$), and older than one year (Fig. 4.4b, $x^2_1 = 1.66$, $P = 0.20$) were the same. Within both species, there were differences between the age classes (yellow mongooses: $x^2_2 = 11.66$, $P = 0.003$; meerkats: $x^2_2 = 5.01$, $P = 0.082$). According to post hoc tests (chi-square tests with Bonferroni corrections), survival rates were similar for yellow mongooses below six months of age and those between six months and one year old ($P > 0.05$), and both these age classes survived better than adults ($P < 0.05$). Although there was a similar pattern in meerkats, differences between age classes were not significant ($P > 0.05$).
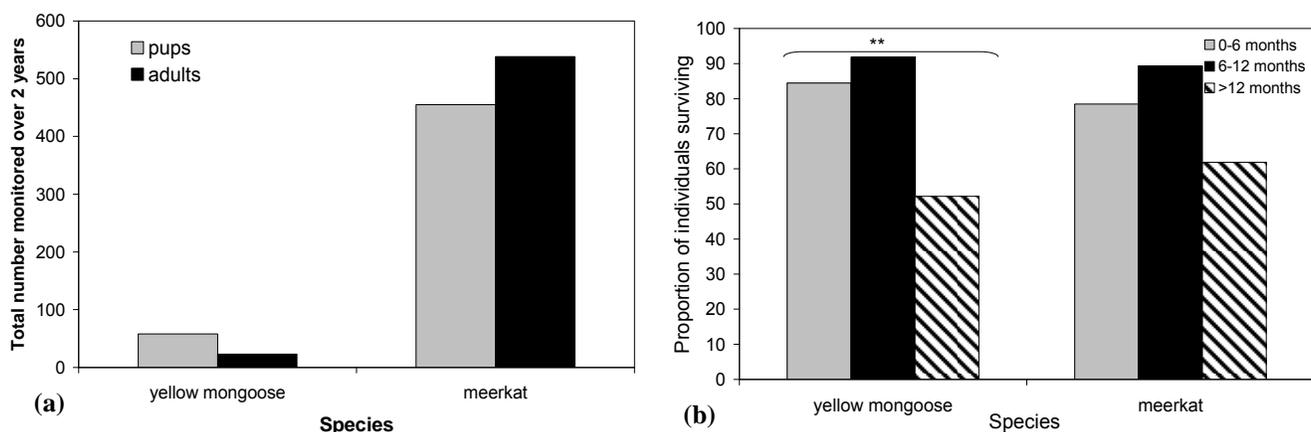
Figure 4.4. Fitness data of yellow mongooses and meerkats in the same area over the same two year period. **a)** Absolute number of individuals born and adults monitored; **b)** Survival rates at different ages (indicated in legend). Differences between species were not significant for any age class. Yellow mongoose survival rates differed between age classes (** $P < 0.01$). Individuals older than one year had lower survival than those up to six months old, and from those between six months and one year of age (post hoc tests: $P < 0.05$).

4.5. DISCUSSION

In contrast to classical predictions of the group-size effect, the duration of active vigilance was equal between the solitary foraging yellow mongoose and group foraging meerkat, and the two species experienced a similar degree of foraging success. Our results confirm Cowlishaw et al.'s (2004) prediction that vigilance will not adhere to the group-size effect if foraging and vigilance are not mutually exclusive behaviours. By mostly having a horizontal head position while foraging and eating, yellow mongooses employed a foraging pattern that allowed them heightened vigilance without detracting from foraging time or efficiency. Yellow mongooses moved fast in a stop-start pattern of locomotion, similar to that of other small mammals (grey squirrels, *Sciurus carolinensis*, and eastern chipmunks, *Tamias striatus*: McAdam & Kramer 1998). Such multiple pauses probably increased the likelihood of detecting predators, but they were too brief to affect mongooses' visibility to predators (sensu Kramer & McLaughlin 2001).

In contrast to yellow mongooses, meerkats foraged with their heads down and primarily displayed costly vigilance in the form of bipedal guarding. Meerkats employ coordinated vigilance as part of their foraging strategy, with a sentinel system (Manser 1999) also described for some other social species (Wright et al. 2001; Bednekoff & Woolfenden 2003). Due to vocal coordination between group members (Manser 1998; 1999) and a sophisticated, referential alarm calling system (Manser 2001), meerkats can respond accurately to the warning behaviour of group members. This coordination allows meerkats to spend more time with their heads down. Yellow mongooses forage for the same food items as meerkats and could pick up more 'surface' items in a short time than could meerkats, but they may miss opportunities for detecting rare, large prey items that meerkats find through improved visual or palpating detection (Glaser 2006). The contrasting foraging 'speeds' of the two species may be a way for both to optimise their fitness in an area where they exploit the same habitat and very similar prey types.

Both species were affected by habitat features and individual risk perception. By staying closer to cover and safe refuges, yellow mongooses and meerkats increased their relative safety rather than their vigilance, similar to rodents such as the degu, *Octodon degus* (Lagos et al. 1995). In other small mammals such as spiny rats of the genus

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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. Experienced, older yellow mongooses were generally more vigilant than younger animals while out in the open. Similarly, fledgling juncos, *Junco phaeonotus* (Sullivan 1988), and meerkats below one year of age (Hollén et al. unpublished data), have lower rates of scanning than adults. This may be a sign of inexperience on the part of immature animals that do not yet display mature vigilance patterns. In yellow mongooses, the presence of predators caused an increase in vigilance, as has been demonstrated for other small mammals (e.g. thirteen-lined ground squirrels, *Spermophilus tridecimlineatus*, Arenz & Leger 1997). Meerkats tended to respond to the presence of predators by frequent, interruptive flights towards safety (see also Manser 2001). This is similar to bird species where cooperative species are more flighty than noncooperative species, probably due to increased, socially-facilitated predator detection (Blumstein 2006).

Both of our study species were affected by the behaviour and presence of group members. Yellow mongooses increased vigilance as individuals went from a solitary to group foraging state, and stayed much closer to boltholes when in a group. Such an increase in vigilance is also found in wild boars, *Sus scrofa* (Quenette & Gerard 1992), when individuals change from solitary to social foraging. Quenette and Gerard (1992) proposed that this was due to a process of allelomimesis, in which animals mimicked group members and increased vigilance because conspecifics were vigilant. However, the guarding behaviour of conspecifics did not affect the vigilance of yellow mongooses. It is also unlikely that individuals were guarding against competition over large prey items, (such as rodents, Cavallini 1993b), as foraging competition away from sleeping burrows was rarely observed in this population, and large prey items seldom found (le Roux, pers. obs.). Groups of yellow mongooses did not detect more predators than solitary individuals (chapter three), but groups were probably more conspicuous than solitary individuals, which may have increased their general nervousness. In contrast, meerkats' individual vigilance decreased when more group members were on guard (unless the group bunched together and became more nervous), and an increase in group size leads to lowered active vigilance in individuals (Clutton-Brock et al. 1999a, Kalahari Meerkat

Project unpublished data). Whereas yellow mongoose nervousness increased and foraging success declined when group members were around, meerkats appeared to benefit from the presence of more, alert conspecifics.

The qualitatively different vigilance strategies used by the sympatric yellow mongooses and meerkats did not have an influence on their comparative fitness. Yellow mongoose and meerkat pups had an equal chance of reaching adulthood, perhaps because yellow mongoose pups benefit from a tendency to forage in groups. Adult yellow mongooses and meerkats had similar survival rates, which were lower than those of their young. Occurring in the same area, eating similar food, and showing similar survival rates, yellow mongooses' and meerkats' distinct group sizes at this study site probably reflect very different optimal foraging-group sizes for these species. Meerkats tend to forage in sizeable groups, as small groups have a high risk of dying out due to predation (Clutton-Brock et al. 1999a). In contrast, yellow mongoose foraging groups remain small across their distribution range (one to three individuals: Nel & Kok 1999) even though larger groups share territories amicably in areas of high food availability (Earlé 1981; Balmforth 2004).

Yellow mongooses are apparently incapable of capitalizing on abundant, renewable invertebrate food resources (sensu Waser 1981) by foraging socially – this is ascribed to 'phylogenetic inertia' by Nel & Kok (1999). Reproductive and social behaviours do not constrain denning group size, as females are polyestrous (Rasa et al. 1992), and individuals in large groups display cooperative alloparental care (Balmforth 2004) and territory defence (Wenhold & Rasa 1994). We postulate that yellow mongooses and meerkats have developed specialized vigilance strategies that have become resistant to change. The ancestral herpestid was purportedly solitary (Veron et al. 2004, Perez et al. 2006), and we suggest that the solitary foraging patterns and lack of group co-ordination of the yellow mongoose are behaviours that have become fixed over a long period of time. The social foraging strategies of the meerkat and other social species are probably more recent developments within the family, as social species diverged from the solitary ancestors in the early Pleistocene (Veron et al. 2004; Perez et al. 2006). These social foraging strategies appear to be an inflexible behavioural pattern as well. Meerkats, for example, are incapable of using low cost vigilance strategies when

group size is reduced, resorting to unsustainably high levels of high cost vigilance (Clutton-Brock et al. 1999a). In the herpestids, where improved anti-predator defence is cited as a primary benefit of sociality (Gorman 1979; Rood 1986), different species' patterns of vigilance behaviour appear to impose rigid constraints on foraging group size, thereby affecting the potential development of sociality.

CHAPTER FIVE

THE EFFECT OF POPULATION DENSITY AND SOCIALITY ON SCENT MARKING IN THE YELLOW MONGOOSE

(A. le Roux, M. I. Cherry, M. B. Manser)
(Journal of Zoology, in press)

5.1. ABSTRACT

We investigated scent marking behaviour in the yellow mongoose, *Cynictis penicillata*, focusing on a low density population where all offspring dispersed upon reaching sexual maturity. Dominant males were the main territory defenders and demarcators, with offspring foraging and marking only near the territory cores. Dominant males used anal marks as predominant form of marking, and latrines appeared to serve as points of information exchange at territory borders. Cheek marking rates of dominant males increased during the breeding season and may have been involved in olfactory mate guarding. We compared our low density population with a high density population displaying natal philopatry (Wenhold & Rasa, 1994). In neither population did the dominant females contribute to territory defence or marking at the border. The two populations differed markedly in terms of individual contributions to territorial marking, as subordinate group members in the low density population performed almost no territorial marking or defence, but were the primary scent markers and territory defenders in the high density population. We discuss scent marking distinctions between populations in the context of ecological and social differences, such as territory size and frequency of intergroup encounters.

5.2. INTRODUCTION

Scent marking behaviour forms an integral part of the communicative repertoire of many mammals (Eisenberg & Kleiman 1974; Gorman & Trowbridge 1989). Scent-marking rates typically increase around the onset of puberty (e.g. Woodmansee et al. 1991), and individuals' scents are often distinct, with many mammals being able to discriminate between individuals on the basis of scent alone (Swaisgood et al. 1999; Mendl et al. 2002; Mateo 2006). In solitary as well as social mammals, scent marks are usually implicated in two primary functions, i.e. territory demarcation – a 'territory' most commonly defined as a defended home range (Maher & Lott 1995) – and sexual advertisement. Dominant males or territory holders typically mark and actively defend

their territories (Ralls 1971). Scent marks serve as information exchange points (Eisenberg & Kleiman 1974), containing, *inter alia*, information on the ability of an owner to defend its territory (Rich & Hurst 1999). During the breeding season, this information includes indications of oestrus in females (Randall 1986), and males may also increase signaling during this season as a form of sexual advertisement (Kappeler 1998). In some species, the male may attempt to mask the female's sexual advertisement by overmarking her scent marks, thereby performing mate guarding (Roberts & Dunbar 2000; Lewis 2005).

In solitary animals, age, gender and territory ownership appear to be the main determinants of scent marking rates, whereas social mammals are, additionally, affected by position in the dominance hierarchy, relative contributions to territory defence, and the frequency of aggressive interactions. Although the dominant male in a group is usually the primary scent marker, subordinate adult group members often contribute substantially to marking and defending the territory, e.g. in coyotes, *Canis latrans* (Gese & Ruff 1997), and meerkats, *Suricata suricatta* (Jordan et al. 2007). Dominance interactions (Shimozuru et al. 2006) or encounters with intruders (Miller et al. 2003), may lead to lower scent marking rates in the defeated individuals. Conspecific scent marks could also be overmarked, either as a form of olfactory mate guarding when a male overmarks a female's scent (Brashares & Arcese 1999b), or in establishing intrasexual dominance, where males overmark subordinate males' scents (Rich & Hurst 1999). Within a social group, allomarking – marking other individuals, instead of the substrate – often occurs, to establish a familiar group smell and maintain tolerance between group members (e.g. in the European badger, *Meles meles*, Buesching et al. 2003).

As there may be great intraspecific variation in territory size, group composition and degree of sociality in vertebrates (Lott 1991), scent marking behaviour within a species is potentially variable. Scent marking strategies of hyenas in different populations diverge markedly depending on territory size. Whereas marks are concentrated in the territory core of large territories (the 'hinterland' marking strategy), they are concentrated along the borders (border marking strategy) of smaller territories (Gorman & Mills 1984). These distinct strategies are seen as the most economical means of marking a territory, ensuring that intruders will come across a scent mark before reaching the protected

territory core. However, few studies have performed intraspecific comparisons of scent marking behaviour between populations with different territory sizes, and in particular, no intraspecific comparisons between populations that show different social structures.

The yellow mongoose, *Cynictis penicillata*, varies from being solitary (Lynch 1980) to facultatively social (Earlé 1981; Balmforth 2004) across its distribution range. Groups denning together vary from 2 to 13 in size, but yellow mongooses typically forage alone or in pairs (Rasa et al. 1992; Cavallini 1993b). The yellow mongoose is territorial and uses various forms of marking in its territory (Earlé 1981; Wenhold & Rasa 1994). Primary forms of marking behaviour are anal marking (marking of vegetation or other prominent objects with the anal gland), cheek marking ('cheek wipes' of vegetation or other prominent objects), and body rubbing ('sidewipes' of vegetation or other prominent objects, including faeces) (after Earlé, 1981; Wenhold & Rasa, 1994). Urination and defecation are secondary forms of marking, and often occur in latrines. Scent marking behaviour in the yellow mongoose has been described in varying degrees of detail in populations of intermediate to high densities [23 – 26 individuals per km^2 (Balmforth 2004) to 133 – 200 individuals per km^2 (Earlé 1981; Wenhold & Rasa 1994)]. Of these studies, Wenhold and Rasa's (1994) was the only one to quantify the marking behaviour of a group of mongooses ($n = 13$ group members) precisely enough to formulate and test specific hypotheses. Whereas Wenhold and Rasa (1994) showed that subordinate adults were the primary territory defenders and markers, using a border marking strategy (sensu Gorman & Mills 1984), Earlé (1981) found that the dominant males played the main role in this respect. This difference is especially striking as both studies focused on the same Big Island (BI) population in the Vaal Dam (26º52'S, 28º11'E), South Africa. Earlé (1981) reported daily allomarking of group members, but allomarking was rare in Wenhold and Rasa's (1994) study group as well as Balmforth's (2004) medium density population.

We focused our research on a low density population of yellow mongooses at the Kuruman River Reserve (KRR) in South Africa, where individuals foraged alone, encountered family members on a daily basis, and rarely interacted with neighbours. The mated pair were the only adult members of each group; offspring dispersed when reaching sexual maturity, and were not involved in raising new litters. Similar to other

low density populations (Cavallini 1993b), aggression between family members and neighbours were very low – few individuals bore any scars marking violent encounters. In contrast, groups in the BI population consisted of the mated pair, recent offspring and related adults that cooperated in the rearing of young and aggressive territory defence (Earlé 1981; Wenhold 1990; Wenhold & Rasa 1994).

Here we describe the scent marking behaviour of the KRR population and compare it with the scent marking behaviour of the BI population (Wenhold & Rasa 1994). We predicted that, as in many mammals (Ralls 1971), the dominant male would be the main territory defender in terms of scent marking and active defence. As territory sizes were much larger in the KRR than the BI population, the KRR population may use a hinterland marking strategy. We did not expect the adult females or offspring to show strongly territorial behaviour. We predicted that offspring would show no evidence of sexual advertisement, as they rarely encountered potential mates prior to dispersal, and did not stay in the natal territory once sexual maturity was reached.

5.3. METHODS

We studied a habituated population of wild yellow mongooses at the Kuruman River Reserve (28°58'S, 21°49'E), South Africa. The study area included the dry Kuruman River bed and surrounding dune areas, primarily covered in low shrubs, *Acacia* trees and grasses (Clutton-Brock et al. 1998; 1999a). The field site had a large number of boltholes and potential sleeping burrows (Manser & Bell 2004) maintained and used by yellow mongooses, meerkats, and Cape ground squirrels, *Xerus inauris*. During the study period from February 2004 to March 2006 data were collected for six adult (dominant) males and 10 of their offspring (four male, six female). Offspring were classified as pups (0 – 3 months), juveniles (3 – 6 months) and subadults (up to 12 months), and adults were older than one year of age. We were able to follow all these habituated animals at a distance of less than 5 m (chapter three), which enabled us to accurately record every scent marking act. We obtained only limited data from one adult (dominant) female.

During active foraging periods we recorded the position of focal animals at ten-minute intervals and the location of all scent marks, using all-occurrence sampling, on an eTrex Garmin[®] Global Positioning System (GPS), to an accuracy of < 10 m. Observational data were collected using a handheld computer (Psion organiser II model LZ64). Each scent marking act was typically preceded by sniffing the object to be marked. We described the object (or individual) marked and whether or not it was within 2 m of a bolt-hole or sleeping burrow. Latrines were defined as defecation points containing three or more faeces within a half-metre radius, and were marked with small flags for identification in case of later re-use. During morning observation sessions we noted all marking acts from the time of emergence, but hourly marking rates were determined using only data from active foraging periods away from the sleeping burrow in the morning and afternoon. Some marking occurred at the sleeping burrow before foraging trips, and these data were included in the ArcView GIS data which we used to determine scent mark densities.

Spatial data were analysed using ArcView GIS and its Animal Movements extension (Hooge et al. 1999). Using all coordinates recorded at ten-minute intervals, we determined home range sizes as the 95% kernel, with least-squares cross-validation smoothing factors (Worton 1989; Seaman et al. 1999). Although autocorrelation between successive data points has been shown to reduce the accuracy of home range estimations (Swihart & Slade 1985), we used a data collection protocol that allowed us to retain all these data in our calculations. The effect of autocorrelation is typically addressed by subsampling the spatial dataset (e.g. Jordan et al. 2007). However, de Solla, Bondruriansky & Brooks (1999) demonstrated that using the entire dataset could improve home range estimations substantially, compared to sub-sampling, if data were collected with a constant sampling interval over an extended period of time. Our regular data collection spanning several months satisfied these recommendations and the number of GPS points per individual (dominant males: 310 ± 26.3 (mean $\pm$ SE); offspring: 115 ± 17.4; dominant female: 80 points) exceeded the recommended minimum of 50 points for home range estimations (Seaman et al. 1999).

We defined adult males' home ranges as territories, as these areas were defended against intruders from other groups (Maher & Lott 1995). The areas occupied by

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offspring and the dominant female were termed home ranges, as we never observed intruder defence in these locations. We defined core and border areas (Fig. 5.1) following Jordan and colleagues' (2007) categorization of meerkat territory areas at the same study site. The area between the 85% and 95% kernel was the 'territory border' and the 65% kernel was the 'territory core.' The area between the territory border and core was the 'kernel border.' Densities of scent marks were calculated for each of these areas and also for the whole area inside the border (i.e. the entire 85% kernel).

Scent mark densities (number of marks per km^2) were calculated from ArcView GIS data and hourly marking rates (number of marks per hour) were determined from *ad libitum* data collected during foraging periods. Due to small sample sizes, we used mainly nonparametric statistical techniques (Siegel & Castellan 1988), in the program R for Microsoft Windows, version 2.3.1 (R Development Core Team 2006). When *t*-tests were appropriate, we used unequal variance *t*-tests of the ranked data (Ruxton 2006). Results are all presented as mean $\pm$ SE. During the summer season we could not record all movement patterns and activities, for individuals were usually highly active after sunset and impossible to follow even with night vision goggles. In summer, adults were primarily babysitting at the sleeping burrow during daylight hours and started foraging late in the afternoon, not returning from foraging and, presumably, scent marking, until after dark. Out of 201 summer observation sessions, mainly focused on habituation, we obtained eight *ad libitum* foraging sessions in total, for three adult males. This number of sessions was too small to compare statistically with the 6 – 14 sessions per adult male (*n* = 6) obtained for each of the other seasons.
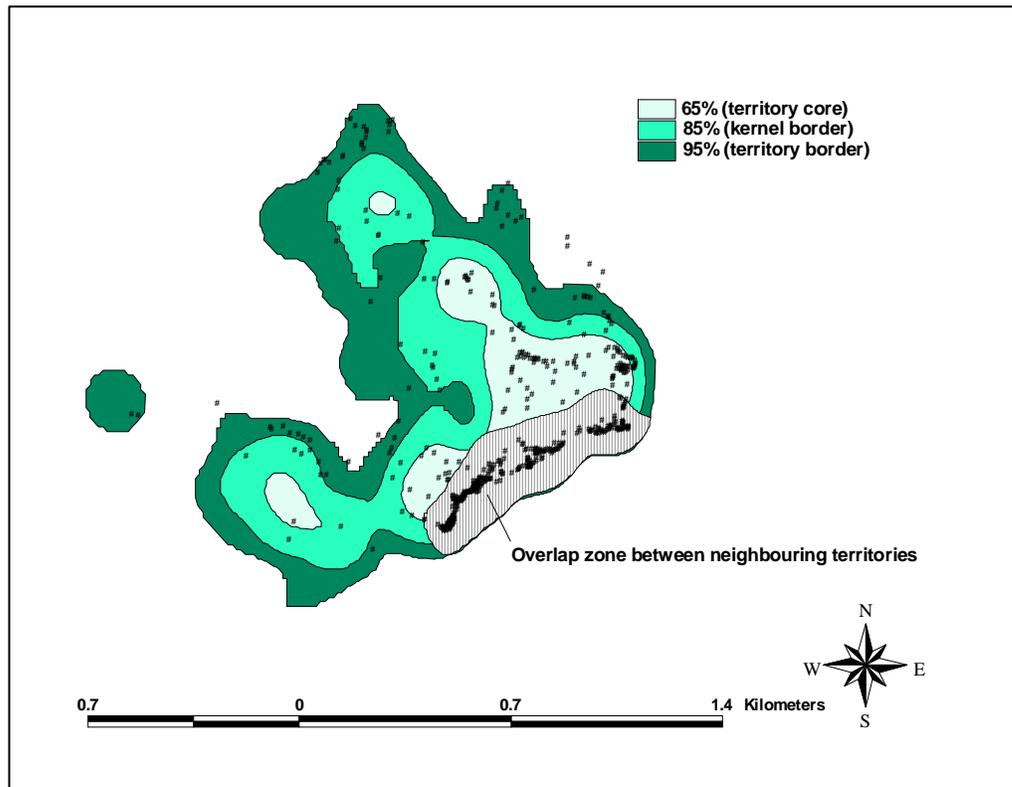
Figure 5.1. The main subdivisions of territory areas are shown for dominant male CM03. Anal marks indicated by filled circles. Higher density of anal marks is in the area where neighbouring territories overlapped.

5.4. RESULTS

5.4.1. Home Range Sizes and Scent Mark Locations

Yellow mongoose densities in the KRR population varied between four and 14 individuals per km^2, depending on season. Groups consisted of 3.7 ± 0.4 members, including offspring, and group size varied from two to seven individuals. Dominant male territories were 0.76 ± 0.21 km^2 in size ($n = 6$), ranging between 0.17 and 1.53 km^2, with a perimeter length of 5.49 ± 0.96 km. These territory sizes remained constant across seasons. Each male's territory completely encompassed the home ranges of his offspring, which were far smaller at 0.18 ± 0.20 km^2 ($n = 10$; range: 0.11 - 0.28 km^2) with a 2.34 ± 0.19 km perimeter length. The only dominant female that we followed had a home range

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size of 0.20 km^2 (perimeter length: 3.05 km) near the centre of her mate's territory, which was 1.11 km^2 in size. Dispersing animals established new territories 2.5 ± 0.4 km ($n = 6$) from their natal territories.

Forty-eight percent of all latrines were within 2 m of a bolthole or sleeping burrow, and active sleeping burrows were characterized by the presence of fresh latrines just outside burrow entrances. Groups had 14.5 ± 2.0 latrines each that were used by all group members in the vicinity of sleeping burrows, and only by adult males outside the territory cores. Activities at latrines (presented as a percentage of all acts at latrines) were primarily defecation (51.1%) and urination (16.1%). Latrines were also sniffed (14.0%), anal marked (11.2%), cheek marked (4.2%) and body rubbed (3.5%). We were able to record the activities of neighbours at shared border latrines for only three latrines. At these latrines the primary act (as a count out of 15 recorded acts) was sniffing (8), followed by defecation (2), urination (2), anal marking (2) and body rubbing (1).

5.4.2. Territorial Defence

Territorial demarcation and defence were not communal acts – only the dominant males patrolled territory borders, whereas their offspring remained within a smaller area inside the males' territories, marking at low rates (Table 5.1). The glandular scent marking rates of dominant males were significantly higher than those of their offspring (unequal variance t-test: anal marks: $t_{15.9} = 6.97$, $P < 0.001$; cheek marks: $t_{12.0} = 4.33$, $P < 0.001$; body rubs: $t_{10.0} = 5.60$, $P < 0.001$). However, defecation ($t_{7.9} = 1.50$, $P = 0.17$) and urination rates ($t_{11.5} = 2.13$, $P = 0.056$) were similar between dominant males and offspring.

A number of differences were evident in the density of dominant males' scent marks throughout their territories (Table 5.2). Anal marks in the territory core were denser than in the territory border as well as in the kernel border, but denser on the territory border than in the kernel border (KW Anova: $\chi^2_2 = 12.43$, $P = 0.002$; post hoc tests: $P < 0.05$). There were no differences between these areas in cheek mark density ($\chi^2_2 = 4.53$, $P = 0.104$) or 'body rub' density ($\chi^2_2 = 4.10$, $P = 0.129$). Defecation points were denser in the territory core than the kernel border ($\chi^2_2 = 8.20$, $P = 0.017$; post hoc tests: P

< 0.05). Similarly, urination points in the territory core were denser than in the kernel border ($\chi^2_2 = 8.84$, $P = 0.012$; post hoc tests: $P < 0.05$). Offspring marked only inside their home ranges, which were contained within the larger territories of the dominant males.

Table 5.1. Average scent marking rates (marks per hour, mean $\pm$ SE) for the dominant males ($n = 6$), offspring ($n = 10$), and one dominant female habituated at the Kuruman River Reserve. Significant differences were found between dominant males and offspring in terms of glandular marking rates.

Identity	Anal mark	Cheek mark	Body rub	Faeces	Urine
Dominant male	9.11 $\pm$ 2.01	4.80 $\pm$ 1.13	1.89 $\pm$ 0.47	0.94 $\pm$ 0.14	0.68 $\pm$ 0.14
Offspring	1.08 $\pm$ 0.22	0.80 $\pm$ 0.56	0.28 $\pm$ 0.14	0.68 + 0.08	0.42 + 0.06
Adult female	1.02 $\pm$ 0.60	0.55 $\pm$ 0.28	0.04 $\pm$ 0.04	0.56 $\pm$ 0.18	0.15 $\pm$ 0.07

Table 5.2. Dominant male ($n = 6$) scent mark densities, presented as number of marks per km^2 (mean $\pm$ SE). Different parts of territories are based on kernel methods (elaborated in text and Fig. 5.1).

Type of mark	Territory core (65% kernel)	Kernel border (65 - 85%)	85% kernel	Territory border (>85% kernel)
Anal mark	1391.1 $\pm$ 784.4	145.2 $\pm$ 22.3	640.6 $\pm$ 284.4	258.8 $\pm$ 37.9
Cheek mark	881.0 $\pm$ 576.2	142.1 $\pm$ 97.5	432.0 $\pm$ 270.6	162.0 $\pm$ 63.0
Body rub	213.3 $\pm$ 91.1	24.1 $\pm$ 15.1	103.7 $\pm$ 44.3	37.5 $\pm$ 12.3
Faeces	87.8 $\pm$ 22.1	15.4 $\pm$ 5.8	45.5 $\pm$ 9.7	25.1 $\pm$ 10.1
Urine	83.0 $\pm$ 38.0	7.2 $\pm$ 1.9	37.4 $\pm$ 12.8	22.4 $\pm$ 9.9

5.4.3. Sexual Advertisement: Seasonal Changes and Overmarking

There was some seasonal variation in the hourly marking rate of adult males (Fig. 5.2), but offspring's marking rates did not vary across seasons (Fig. 5.3). Dominant males' cheek marking rates differed between seasons (KW Anova: $\chi^2_2 = 8$, $P = 0.018$) due to spring rates being higher than autumn rates, and body rubbing rates differed in the same respect ($\chi^2_2 = 6.26$, $P = 0.044$). Anal marking rate did not differ between seasons ($\chi^2_2 = 3.14$, $P = 0.208$), nor did defecation ($\chi^2_2 = 0.56$, $P = 0.756$) or urination rate ($\chi^2_2 = 3.98$, $P = 0.137$). Summer marking rates were 1.9 ± 0.7 for cheek marks, 7.1 ± 2.0 per hour for anal marks, 2.5 ± 0.8 for body rubs, 0.4 ± 0.2 for defecation, and 0.3 ± 0.1 for urination points. None of the offspring's marking rates (Fig. 5.3) were affected by month of the year or age, although defecation rates showed a non-significant trend to increase by month, most likely because individuals' body size increased (linear mixed-effects model: $F_{denDF = 34} = 4.01$, $P = 0.053$; Odds Ratio = 1.057).
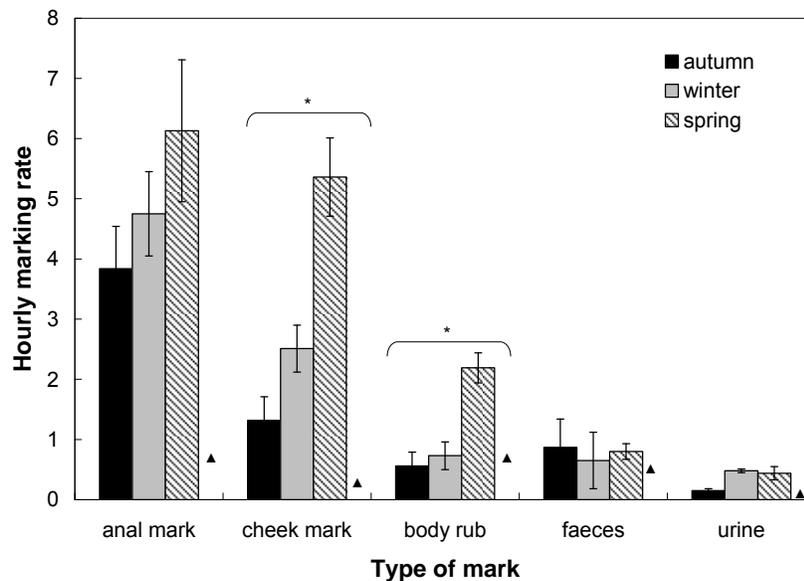
Figure 5.2. Dominant male scent marking rates as affected by season (* $P < 0.05$). Filled triangles represent marking rates of dominant males in a high density population (after Wenhold & Rasa 1994).
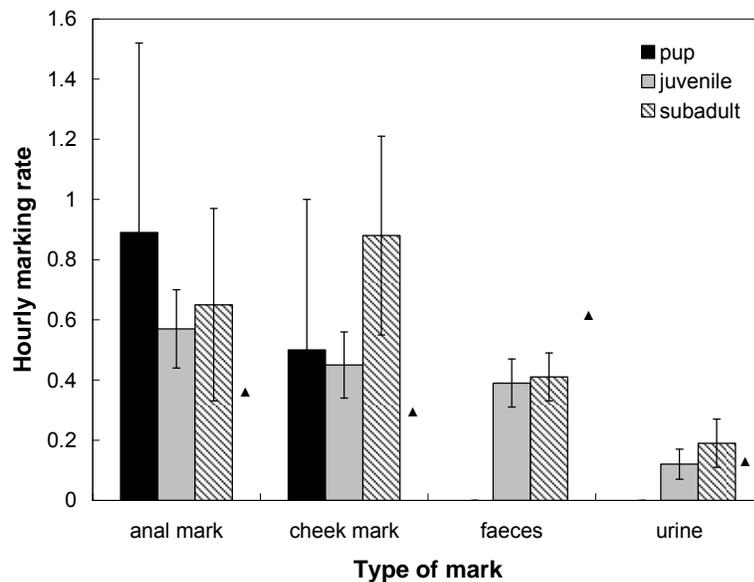
Figure 5.3. Offspring scent marking rate depending on age class. Scent marking rates were not affected by age or season. Filled triangles are marking rates for 'juvenile' (< 1 year old) yellow mongooses in a high density population (after Wenhold & Rasa 1994).

The areas close to sleeping burrows were marked by all group members, but no overmarking was observed between adults and offspring, even though group members were observed foraging together. We did not observe the dominant female and her mate foraging together, but the area where she deposited most of her cheek marks was a location where her mate concentrated a high number of cheek marks (15 marks in a 10 m radius). Her anal marks were in an area where the male also anal marked, but the closest male anal mark was 20 m from her marks.
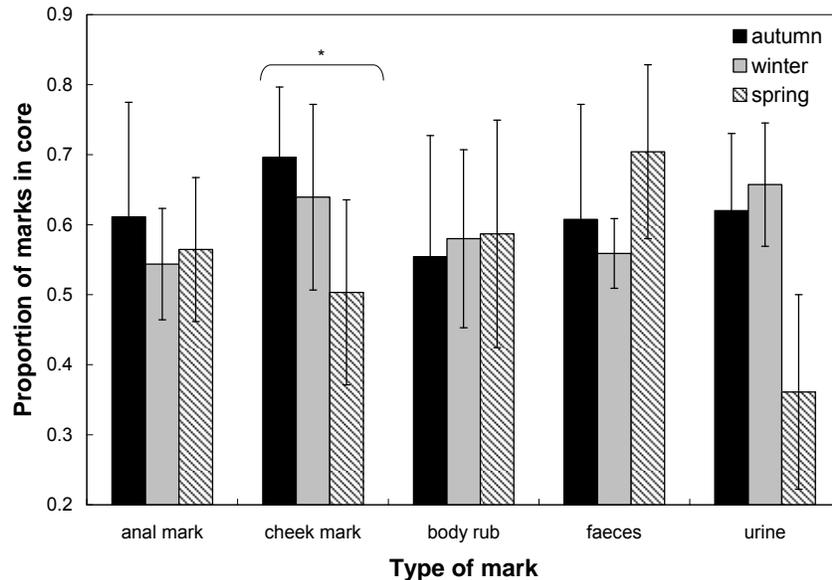
Figure 5.4. The proportion of dominant male scent marks that were made inside territory cores, according to season. The proportion of cheek marks inside the territory core was significantly smaller in spring than in winter and autumn. (* $P < 0.05$)

When offspring dispersed (spring season), dominant male marking rates increased (Fig. 5.2). However, this increase was not focused specifically in the territory core, where offspring used to mark. Between 50 and 70 % of marks were made in the territory core, (Fig. 5.4) and remained similar across seasons for anal marks (Friedman Anova: $\chi^2_2 = 0.4$, $P = 0.819$), body rubs ($\chi^2_2 = 0.4$, $P = 0.819$), defecation ($\chi^2_2 = 2.8$, $P = 0.247$) and urination points ($\chi^2_2 = 4.0$, $P = 0.353$). Cheek mark distribution varied, however ($\chi^2_2 = 7.6$, $P = 0.022$), as winter and autumn proportions were significantly higher than spring proportions (post hoc tests: $P < 0.05$). Relatively more cheek marks were therefore located outside the territory core during spring.

5.5. DISCUSSION

5.5.1. Territoriality

In the low density KRR population only the dominant males defended and marked their territories, in contrast to the high density BI population, where subordinate individuals as well as dominant males maintained territory borders (Earlé 1981; Wenhold & Rasa 1994). Although the dominant male is usually the main scent marker in obligate social carnivores, group members often contribute substantially to territory defence and scent marking, for example in Ethiopian wolves, *Canis simensis* (Sillero-Zubiri & MacDonald 1998), and meerkats (Jordan et al. 2007). Group defence occurs together with other cooperative behaviours, such as the communal rearing of young by subordinate adult wolves (Sillero-Zubiri & Gottelli 1994) and meerkats (Clutton-Brock et al. 2001a). Unlike the low density population, philopatric mongooses in the high density population not only share the mated pair's territory, but contribute to the rearing of their subsequent litters (Wenhold 1990; Balmforth 2004), which may explain why their pattern of territory defence resembles that of obligate social carnivores.

Dominant males in the low density population had high marking rates compared to individuals in the high density population. However, if all group members' contributions were taken into account, group scent marking rates were similar between the high (Wenhold & Rasa 1994) and low density populations. Contributions of group members allowed dominant males to defend their small territories in the BI population by using the border marking strategy (sensu Gorman & Mills, 1984). The hinterland marking strategy (Gorman & Mills, 1984) employed by dominant males in the KRR population is used by other carnivores such as solitary honey badgers, *Mellivora capensis* (Begg et al. 2003), and social meerkats (Jordan et al. 2007). It is probably a reflection of the need to protect core resources, such as sleeping burrows and feeding sites, in large territories where intruders may not come across border marks while traveling through an area (Gorman & Mills 1984; Jordan et al. 2007).

As with other herpestids (Rasa 1973; Baker 1982; 1988a), anal marking was the predominant form of territorial marking in yellow mongooses. Anal gland secretions in

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the yellow mongoose (Apps et al. 1989) and other herpestids function as long lasting markers carrying information on individual identity (Rasa 1973; Hefetz et al. 1984; Decker et al. 1992). In both populations of yellow mongooses, territory defenders augmented their own scent by body rubbing, spreading it across their fur (Wenhold & Rasa 1994). Dominant males in the KRR population increased body rubbing rates during spring, when intruder pressure increased as dispersers attempt to found new territories. Males also had high anal marking and body rubbing rates after dispersal, while establishing new territories. The combination of anal marking, border latrines, and body rubbing, could function as a scent matching system of territory defence (Gosling 1982), whereby intruders match the scent of territorial marks with the scent of the owner when encountering this individual. Recognition of ownership reduces the aggression of agonistic interactions, to the mutual advantage of intruder and owner (Gosling & McKay 1990).

Aggression between familiar neighbours appeared to be low in the KRR population. There were few fights between neighbours, almost no visible scars on adult males, and territory expansion into neighbouring territories was never observed. At shared borders, latrines elicited a high rate of sniffing, likely serving as points of information exchange, similar to the latrines of other territorial carnivores (Begg et al. 2003; Jordan et al. 2007). Preliminary experiments with fresh faeces from foreign (non-neighbouring) males (A. le Roux, unpublished data) indicated that latrines consisting of foreign faeces, representing the long term presence of an intruder, always provoked an immediate countermarking reaction. Such a tolerance of familiar neighbours, with higher aggression against unfamiliar intruders, is known as the 'dear enemy' effect (Fisher 1954), and occurs in a variety of territorial species (reviewed in Temeles 1994). This contrasts with the 'nasty neighbours' effect found in, for example, banded mongooses, *Mungos mungo* (Müller & Manser 2007), that treat neighbours more aggressively than transients. This aggressive defence is necessary because groups readily expand into neighbouring territories (Müller & Manser 2007). In high density populations of yellow mongooses, intergroup encounters appeared to be more violent and frequent (Wenhold & Rasa 1994; Balmforth 2004). Yellow mongoose groups in high and low density populations have similar combined scent marking rates, but territory sizes are up to five

times smaller in the high density population (Wenhold & Rasa 1994). This means that scent mark densities in the high density population are much higher than the low density population. It is probable that aggression against neighbours and scent mark densities are increased in high density populations as territory reduction is a definite risk in environments with high territory saturation.

5.5.2. Sexual Advertisement?

In the low density population there was no support for Wenhold & Rasa's (1994) hypothesis that scent marking is used as sexual advertisement by subordinate individuals. Whereas mongooses in the BI population found mating opportunities in neighbouring groups (Wenhold & Rasa 1994), sexually mature offspring in the KRR population dispersed to new territories beyond neighbouring groups. The marks of offspring in the low density population may, however, have functioned in intragroup communication. Allomarking, displayed by high density yellow mongoose populations (Earlé 1981) and social mongooses such as the dwarf mongoose, *Helogale undulata rufula* (Rasa 1973), was extremely rare in the KRR population. Although no 'group odour' (sensu Ropartz 1966; Sheppard & Yoshida 1971, in rodents) appears to exist, dominant males may have become more familiar with offspring's scent through marks they encountered. In other group-living mammals, the familiarity of an individual's scent has been shown to reduce aggression from the dominant male (Huck & Banks 1979). The scent marks of KRR offspring may have facilitated tolerance by the dominant male during the time they shared a home range. In addition, offspring scent marks could have augmented dominant male marks around key resource areas, thereby contributing to territorial defence (Revilla & Palomares 2002). However, dominant males did not 'compensate' for the absence of these marks once offspring dispersed.

Dominant males' cheek marking rates increased when offspring dispersed, but this increase was primarily outside the territory core, and could have been related to higher intruder pressure during this season, rather than the decrease in number of group members. In water mongooses, *Atilax paludinosus* (Baker 1988a), and dwarf mongooses (Rasa 1973) cheek marks appear to carry a short-lived threatening message. During

aggressive interactions between males, scent from cheek glands are probably exchanged, as fighting yellow mongooses attack the face and neck of their rivals (pers. obs.). Yellow mongoose cheek marks were concentrated around boltholes, which are noticeable landmarks regularly inspected by other yellow mongooses, especially adult males. Limited data suggested that a dominant male overmarked the area that his mate cheek marked. It is therefore probable that cheek marks had a function in mate guarding (Roberts & Dunbar 2000; Lewis 2005), although the possibility of male sexual advertisement could not be excluded. The dominant female, which does not mark at the borders of high (Wenhold & Rasa 1994) or low density yellow mongoose populations, may be a 'resource' protected by males within their territories (Ostfeld 1990).

5.5.3. Conclusions

The scent marking patterns of yellow mongooses were affected by the long term group composition within a specific area. In temporary groups where the mated pair were the only long term residents in a territory, marking behaviour resembled that of solitary territorial mammals, with only the dominant male defending and marking his territory. The dominant male may have used cheek marks in olfactory mate guarding. Natal philopatry in high density populations appeared to have implications for increased facultative cooperation that included cooperation in scent marking and intergroup contests. Larger groups in high density populations interacted with neighbours more frequently, causing more conflict but also opportunities for mating and sexual advertisement between neighbours. Although none of these results are unexpected, considering the characteristics of the different populations, this may be the first mammalian study to show how individuals' scent marking patterns vary, specifically, along with intraspecific fluctuations in social structure.

CHAPTER SIX

GENERAL DISCUSSION

The yellow mongoose is perhaps the most thoroughly studied of the nongregarious herpestids. It has been the subject of behavioural studies on low (this thesis), medium (Balmforth 2004), and high density populations (Earlé 1981; Wenhold 1990; Wenhold & Rasa 1994), in addition to a number of studies on ranging and foraging behaviour (Zumpt 1968; Herzig-Straschil 1977; Avenant & Nel 1992; Cavallini 1993b; a; Nel & Kok 1999). Some of its more cooperative behaviours may be shared with both solitary and social mongooses. The flexibility in its group *living* behaviour – the refuging, rearing and mating functional phases of its life (Eisenberg 1981) – may be similar in other nongregarious mongooses, as solitary species such as the slender mongoose (Rood 1989), small grey mongoose, *Galerella pulverulenta* (Cavallini & Nel 1990; 1995) and white-tailed mongoose, *Ichneumia albicauda* (Waser & Waser 1985), exhibit social tendencies in areas where food distribution leads to high population densities. As the behaviours of solitary mongooses in the wild are virtually undescribed, we do not know if the social behaviours of solitary carnivores are in reality more flexible than they are currently presumed to be (Leyhausen 1965; Dalerum et al. 2006). My study has highlighted that we cannot assume that the selective forces leading to the evolution of group living 'automatically' leads to the development of group foraging (see also Carr & Macdonald 1986). This was also recently pointed out by Whitehouse and Lubin (2005), who used social spiders as an example to demonstrate that we need to be more explicit when we distinguish between selection for group living and group foraging. Although sociality, once evolved, usually serves multiple functions, in most taxa it originated to serve either a reproductive, or foraging or protective function, and the assumptions we often implicitly make – that social foraging and living evolved together – are not necessarily true (Whitehouse & Lubin 2005).

6.1. FLEXIBILITY IN COMMUNICATION AND COOPERATION

6.1.1. Vocal Repertoire

The size and complexity of the yellow mongoose's vocal repertoire (chapter two) reflects its social complexity. When the vocal repertoires of solitary, intermediately social, and obligate social mongooses are compared, it appears that social complexity does predict vocal complexity in the Herpestidae (sensu Marler 1967; Wilson 1972). In particular, the yellow mongoose's vocal repertoire supports Schassburger's (1993) specific predictions, i.e. an increased proportion of affiliative vocalizations, larger number of distinct calls, and greater context specificity as sociality increases. Although my study population was not highly social, the vocalizations that individuals used were suggestive of the cooperative social structure that is found in higher density yellow mongoose populations (Earlé 1981; Wenhold 1990; Balmforth 2004). The comparative vocal information we have for solitary species is based mainly on captive studies (Baker 1982; 1988b) and remains highly limited. The descriptions of these vocalizations as primarily aggressive (e.g. for slender mongooses, Baker 1982) stand in contrast with the apparently playful and cooperative behaviour that these mongooses may exhibit in the wild, even amongst adults (Rood 1989). In the light of social tendencies in some other solitary mongooses (Waser & Waser 1985; Cavallini & Nel 1990; 1995), there is a need to elaborate on the descriptions of vocal and social behaviour in wild populations of solitary mongooses. Although gregarious mongooses certainly have large and complex vocal repertoires, the complexity of solitary species' vocal repertoires may have been underestimated.

6.1.2. Territorial Demarcation and Defence

The variability in yellow mongooses' scent marking behaviour can be directly linked to levels of cooperation within a territory. Similarly, in obligate social species, such as the dwarf mongoose, individual scent marking behaviour is directly related to the roles played by that individual within the group (Rasa 1973; 1977). In the yellow mongoose the long-term presence of conspecifics in a territory leads to cooperation in both rearing

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of offspring and territory defence (Wenhold & Rasa 1994; Balmforth 2004). Cooperative behaviour may even lead to a shift in the territorial role of the dominant male. In a high density population (Wenhold & Rasa 1994), the surprising finding was perhaps not that subordinate adults marked and defended the territory borders, but that the dominant male never marked the borders and exhibited lower marking rates than the subordinate adults. This appears analogous to the behaviour of dominant male oribis, *Ourebia ourebi*, that decrease their faecal output when more subordinate males contribute to territorial demarcation (Brashares & Arcese 1999b) – these males therefore 'economize' on scent marking. No long-term study of scent marking behaviour has yet been done on a high density yellow mongoose population. If dominant males do economize when possible, we can expect that these males will increase their contribution to marking and defence when the number of subordinate adults in their group falls. Such a response to the presence or absence of subordinate markers would suggest that dominant animals actively take advantage of the scent marking behaviour of group members, and would confirm variability in the yellow mongoose's scent marking behaviour that is more typical of social rather than solitary mammals.

6.1.3. Alarm Signaling and the Audience Effect

Despite not foraging socially, the yellow mongoose exhibits alarm signaling behaviour and adapts its anti-predator behaviour depending on the presence or absence of conspecifics. This audience effect (chapter three) has not been shown in any other nongregarious mammal, but it is a logical expectation from the definition of true communication. In true communication (Marler 1968; Bradbury & Vehrencamp 1998), it is to the benefit of both sender and receiver that the signal reaches its intended audience. Therefore, the simplest form of the audience effect – adapting signals depending on the presence or absence of conspecifics – should probably be evident in all species that communicate with conspecifics. The more subtle forms of an audience effect – in which the exact nature or composition of an audience affects signaling behaviour (e.g. in chickens, Karakashian et al. 1988) – may, however, not be ubiquitous. This more complex audience effect requires a sender to be aware of exactly which individual/ type

of individual (e.g. male versus female) is present, and may therefore be dependent on past experiences with specific individuals. This may thus be limited to more social species.

There is an unexpected prediction that stems from the presence of the audience effect and alarm signaling behaviour in the solitary foraging yellow mongoose. These behaviours imply that the evolution of alarm signaling behaviour has preceded the evolution of social foraging in herpestids. This prediction could be tested by further elucidation of the vocal repertoires of wild populations of solitary mongooses. In rodents, alarm signaling is present in some solitary species (Shelley & Blumstein 2005). This may be because alarm signals are, firstly, directed at the predator, and only secondarily to conspecifics (Shelley & Blumstein 2005). However, the yellow mongoose's vocal alarm signals, at least, do not appear to be directed at predators, and the evolution of alarm calling in this species suggests gregarious tendencies – the warning of kin (Sherman 1977) – rather than, in the first instance, communication with predators. This may also be the case for other nongregarious herpestids.

6.2. INFLEXIBILITY WHILE FORAGING

In chapter four I have attempted to answer the question that has plagued investigators of herpestid sociality for a long time – why do yellow mongooses forage alone, if they share so many habits with social mongooses? I have proposed that the distinct vigilance pattern of the yellow mongoose is adapted to solitary foraging, and differs from that of social species – specifically, the meerkat's – to such an extent that social foraging is detrimental to the yellow mongoose's vigilance behaviour and foraging success. This is exactly opposite to the expectations of the group size effect. Although the benefits of the group size effect are purely numerical – the detection (Pulliam 1973), dilution (Hamilton 1971) and confusion effects (Vine 1971) do not require active cooperation to function – this effect has primarily been investigated and demonstrated in social species (Inman & Krebs 1987; Elgar 1989; Quenette 1990). The presence of scrounging or competing conspecifics increases vigilance in some mammals (e.g. in primates Treves 2000), but I am not aware of many studies (except for Tchabovsky et al. 2001b) considering the effect of non-

competing conspecifics on the vigilance of solitary species. In species that make use of camouflage and cryptic movement as primary methods of anti-predator defence, we should expect the exact opposite of the group-size effect (Bekoff et al. 1984). In some solitary mammals, such as the fat sand rat, *Psammomys obesus* (Tchabovsky et al. 2001b), the presence of group members may decrease vigilance, but there have very few studies on the group size effect in typically solitary species. The group size effect may be present only in social species (as suggested in chapter four), and should therefore not be seen as a mere 'numerical' phenomenon, but as a social one. Within the Herpestidae, a number of solitary species have been reported foraging with conspecifics (see references above), and such species could be ideal for such future studies of vigilance.

6.3. FUTURE WORK ON THE YELLOW MONGOOSE

There is the potential for much future work on the yellow mongoose, as it is a species that is fairly easy to habituate – away from human disturbance (Z. Balmforth, pers. comm., pers. obs.) – with a flexible social structure and widespread distribution (Mills & Hess 1997). There are still gaps in our knowledge of the yellow mongoose's behaviour. In particular, the female's role in scent marking and territorial defence remains unknown. Females in both high (Wenhold & Rasa 1994) and low density populations (Cavallini 1993b) appear to restrict themselves to small, undefended home ranges contained within the territories of dominant males. However, they may form dominance hierarchies in medium density populations (Balmforth 2004), which should affect their scent marking patterns, and Earlé (1981) has suggested that they do take part in communal defence.

Yellow mongooses appear to be unique amongst herpestids in their system of pup care (Rasa et al. 1992). With both parents – and subordinate adults in a social group (Balmforth 2004) – bringing food to the sleeping burrow and babysitting offspring until the age of about two months, the yellow mongoose never needs to take vulnerable young pups with them on foraging excursions. Young mongooses start foraging independently in their third month of life, and the yellow mongoose does not exhibit pup feeding (Rasa 1989b), escorting (Gilchrist 2004) or teaching (Thornton & McAuliffe 2006) that

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characterize the foraging habits of social mongooses during the breeding season. The yellow mongoose may never have had to protect vulnerable pups while foraging, and this may be an additional reason why there was little selection for social foraging in this species. Amongst the diurnal, open-habitat, invertebrate eating mongooses – all of these, besides the yellow mongoose, being obligate social species (Rood 1986; Veron et al. 2004) – this need to protect and feed young pups may thus have been a primary impetus in the evolution of social foraging. Perhaps social learning or even teaching does occur in the short period of time that yellow mongoose pups are 'baby-sat' at the sleeping burrow. In their willingness to explore novel objects – specifically, new food items – yellow mongoose pups appear bolder and quicker to learn than meerkat pups (pers. obs.). This may be related to the yellow mongoose's more opportunistic diet (Zumpt 1968; Taylor & Meester 1993). However, very little is currently known on the behaviour of yellow mongoose pups, or pup behaviour in solitary mongoose species.

The yellow mongoose appears to show strong awareness of its social environment, and this environment frequently includes heterospecific mammals such as meerkats and Cape ground squirrels. Meerkats and yellow mongooses occasionally forage together amicably and it is highly likely that yellow mongooses are exposed to the complex, functionally referential alarm vocalizations (Manser 2001; Manser et al. 2001) of this social species. Through playback studies, it should be possible to investigate whether or not yellow mongooses show an understanding of the meaning of these vocalizations, even when they do not produce functionally referential alarm calls themselves. It is plausible that the yellow mongoose could show understanding of the alarm calls of other species – similar to the way that dwarf mongooses and hornbills (*Tockus* spp.) react appropriately to one another's alarm signals (Rasa 1983) – and the fact that they do not use an functionally referential alarm call system does not imply that they lack the cognitive capabilities to understand such a system.

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Table 1. Acoustic description of the eight call types used by the yellow mongoose. *N* refers to sample sizes. Subsets of these calls were used in discriminant function analyses, as described in chapter two.

Parameter	Units	Rolling alarm	Peepgrowl: peep	Peepgrowl: growl	Low growl	Chase call	Krr call	Mobbing call	Recruitment call	Mating call
N	none	58	81	59	37	22	49	7	33	31
Duration	s	0.63 ± 0.05	0.15 ± 0.01	1.27 ± 0.05	0.54 + 0.03	0.50 ± 0.08	0.76 ± 0.08	0.39 ± 0.15	0.28 ± 0.03	0.72 ± 0.08
Dur.ratio	none	0.38 ± 0.04	0.47 ± 0.02	0.58 ± 0.03	0.47 + 0.03	0.23 ± 0.08	0.51 ± 0.09	0.34 ± 0.06	0.33 ± 0.06	0.40 ± 0.06
Pf (start)	kHz	315 ± 26	495 + 15	282 + 21	319 + 17	1824 ± 600	662 ± 160	876 ± 419	471 ± 75	411 ± 44
Pf (max)	kHz	310 ± 24	617 + 12	494 + 49	354 + 14	2533 ± 388	678 ± 208	1339 ± 694	789 ± 64	741 ± 151
Fund (mean)	kHz	284 ± 22	549 + 18	412 + 43	320 + 10	1083 ± 350	402 ± 100	235 ± 43	613 ± 87	349 ± 45
Entr (mean)	none	0.28 ± 0.01	0.24 + 0.01	0.31 + 0.01	0.30 + 0.01	0.60 ± 0.04	0.48 ± 0.03	0.47 ± 0.07	0.35 ± 0.01	0.43 ± 0.02
BW	kHz	984 ± 47	995 + 36	1126 + 42	1259 + 31	1358 ± 391	963 ± 272	807 ± 294	645 ± 96	2236 ± 309
L.qrt	kHz	323 ± 15	476 + 12	329 + 10	345 + 10	2127 ± 477	1271 ± 157	1476 ± 440	798 ± 33	526 ± 82
M.qrt	kHz	503 ± 27	591 + 12	502 + 18	521 + 15	3160 ± 505	2352 ± 248	2774 ± 639	1627 ± 229	1053 ± 154
U.qrt	kHz	865 ± 85	846 + 22	810 + 29	869 + 20	3498 ± 667	2576 ± 388	2843 ± 1100	1799 ± 394	1746 ± 207