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# Extraterritorial prospecting and territory defence in cooperatively breeding meerkats

Rafael Mares



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## **PREFACE**

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This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except where specifically indicated in the text. The total length of the text does not exceed 60,000 words. No part of this dissertation has been submitted to any other university in application for a higher degree.

Rafael Mares

4 January 2012

## SUMMARY

# **Extraterritorial prospecting and territory defence in cooperatively breeding meerkats**

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In group living animals where natal dispersal is delayed, prospecting allows individuals to assess their future dispersal and breeding opportunities and, in males of some species, may minimize the costs of delaying dispersal by enabling extra-group breeding while still resident in the natal group. While evidence of prospecting is widespread, comparatively little is known about the development of this behaviour and few studies have investigated the factors that may affect investment in prospecting, as it is typically difficult to monitor such mobile individuals. Prospectors typically encounter neighbouring groups during extraterritorial forays and resident individuals in these groups respond aggressively to approaches by extra-group males, given the potential loss in direct and indirect fitness that prospectors may inflict. As with prospecting behaviour, few studies have investigated the causes of individual differences in investment in repelling prospectors and measured the costs of such territory defence. In this dissertation, I exploit our ability to closely monitor prospecting males in meerkats, to investigate the causes of individual variation in extraterritorial prospecting effort and aggressive responses to prospector intrusions. In Chapter 3, I show that, as adults, heavier males invest more in prospecting than lighter ones, and that males time their forays in order to maximize their chances of dispersal, while minimizing the associated costs by prospecting when neighbouring groups are in close proximity to their own. In Chapter 4, I demonstrate that males that are heavier in early life start prospecting at a younger age and contribute less to helping later in life, than lighter males. In Chapter 5, I show that the threats posed by prospectors towards residents are associated with high investment by resident males in repelling intruders, which has measurable costs in terms of weight gain and cooperative contributions to offspring care. Finally, in Chapter 6, the experimental presentation of scent cues reveals that meerkats discriminate between resident and extra-group male scent cues, and that resident dominant males exhibit stronger responses to indirect evidence of prospectors than other group members.

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## CHAPTER 1

# General Introduction

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In cooperatively breeding species where reproduction is monopolized by a dominant pair, extraterritorial prospecting forays may allow subordinate males not only to assess future dispersal opportunities, but also to mate with extra-group individuals (e.g., Young et al. 2007; Eikenaar et al. 2008). Despite the potential benefits accrued by prospecting, individuals are likely to vary in their investment in these extraterritorial forays as they are expected to be costly. Indeed, resident individuals typically respond to approaches by prospectors with a suite of aggressive behaviours (e.g., Lazaro-Perea 2001; Raihani et al. 2010), as a result of the potential loss in direct or indirect fitness that prospectors may inflict (e.g., Westneat and Stewart 2003). However, contributions to repelling prospectors are likely to be state-dependent and vary between resident individuals (e.g., Heinsohn et al. 1996). As with investment in prospecting behaviour, the extent of variation in investment in repelling prospectors,

along with its causes and consequences, are poorly understood. In this dissertation, I investigate the factors that influence the investment in prospecting behaviour by subordinate males, as well as the factors that modulate individual investment in territorial behaviours involved in the repulsion of prospectors, in cooperatively breeding meerkats.

## **1.1 Overview of extraterritorial prospecting**

Prospecting has been studied primarily in birds as the process by which individuals gather information on possible breeding sites before settling to breed (reviewed in Reed et al. 1999). This information gathering can be stationary (e.g., within a breeding colony) or may entail extraterritorial movements prior to dispersal from the current site or group (Waser 1996; Reed et al. 1999; Danchin et al. 2001). Prospecting from a home territory or group (centrally-based prospecting; Danchin et al. 2001) allows individuals to conduct repeated extraterritorial forays and is most common in cooperatively breeding species (Reed et al. 1999). These temporary forays typically involve visits to neighbouring groups, allowing breeders to access additional extra-group mating opportunities, regardless of whether these prospecting individuals ultimately emigrate or not (e.g., Double and Cockburn 2003; Randall et al. 2007). In addition to breeding individuals, subordinates may also conduct prospecting forays in cooperative breeders, where offspring typically delay dispersal from the natal group (e.g., Du Plessis 1992; Lazaro-Perea 2001; Young et al. 2007).

Prospecting in many species precedes natal and breeding dispersal (Waser 1996; Reed et al. 1999; Danchin et al. 2001), and the information gathered during forays is expected to influence decision making in all three stages of dispersal: emigration, inter-patch movement and immigration (Bowler and Benton 2005; Cote et al. 2010). Prospecting forays, therefore, should lead to informed decisions about settling at specific locations (informed dispersal; Reed et al. 1999; Clobert et al. 2009). Yet, direct evidence for the relationship between prospecting and informed dispersal is scarce (Ward 2005; Mabry and Stamps 2008; Selonen and Hanski 2010; Pärt et al. 2011), not least because following individuals that leave their typical area of use has been challenging (Waser 1996). Substantial indirect evidence supports the link between prospecting and informed dispersal: prospecting birds typically conduct

forays at the end of the breeding season, when information regarding reproductive success is expected to be most accurate, and visit several sites before settling to breed the following year (reviewed in Reed et al. 1999). Furthermore, in group-living species, prospecting forays are typically conducted by individuals that subsequently emigrate from their groups (e.g., Du Plessis 1992; Eikenaar et al. 2008) and repeated forays can ultimately lead to permanent residency at a foreign group previously visited (e.g., Doolan and Macdonald 1996b, Williams and Rabenold 2005).

In addition to gathering information on future dispersal and breeding opportunities, prospecting individuals may be able to enhance their current reproductive success. Mating during extraterritorial forays has been extensively reported in birds, where these forays are likely to explain a majority of the extra-pair paternity observed (reviewed in Westneat and Stewart 2003). Such behaviour also occurs in mammals (reviewed in Waser 1996) and genetic data revealing varying levels of extra-pair paternity in a range of species (Clutton-Brock and Isvaran 2006) could be explained by copulations with prospecting individuals (e.g., Baker et al. 2004; Dugdale et al. 2007). In cooperatively breeding species, where subordinate individuals' reproductive opportunities may be limited within the natal group, owing to a lack of unrelated mates or reproductive suppression (Emlen 1995), prospecting may provide an alternative route to reproduction other than or prior to dispersal, or while queuing for the dominant position within a group. Mating by prospecting subordinate individuals has been documented in a number of cooperative breeders (e.g., Lazaro-Perea 2001; Eikenaar et al. 2008) and mating opportunities arising from prospecting forays may account for a majority of subordinate reproduction (e.g., Double and Cockburn 2003; Young et al. 2007). This mating tactic may provide the additional benefit of allowing individuals to start breeding at an earlier age than would occur by queuing in the natal group or dispersing (Young et al. 2007).

### **1.1.1 When do individuals prospect?**

The timing of prospecting forays may depend on a species' breeding system and the purpose of extraterritorial forays. In their review of prospecting in birds, Reed et al. (1999) focused largely on colonial species and found that prospecting typically occurred at end of the breeding season. Monitoring multiple breeding colonies at the end of the breeding season is expected to allow individuals to assess breeding site

quality for the following year. Alternatively, cooperative breeders may prospect before the breeding season, to assess current dispersal opportunities (Du Plessis 1992); or during the breeding season, to assess current mating opportunities and either disperse the following year (Williams and Rabenold 2005) or not disperse at all (Double and Cockburn 2003). Furthermore, dominants and subordinates may differ in the function and timing of their forays: existing dominants may be prospecting for additional breeding opportunities, while subordinates may be prospecting for both breeding and dispersal opportunities. For example, dominant Micronesian kingfishers prospect during the breeding season, presumably in search of extra-pair mating opportunities, while helpers prospect throughout the year in search of both mating and dispersal opportunities (Kesler and Haig 2007). In general, prospecting among subordinate individuals may be less constrained to peak fertility periods than prospecting by dominants, if assessing mating and dispersal opportunities are equally important.

A further consideration is that prospecting may be energetically costly, and individuals would be expected to mitigate the costs by timing their forays appropriately. Prospecting typically involves travelling alone (or in reduced numbers) and in unfamiliar areas, both of which can potentially increase the risk of predation and have detrimental effects on condition (Waser 1996; Dufty and Belthoff 2001). Prospectors are also typically met with aggressive behaviours from residents in territories visited during forays (e.g., Baker and Dietz 1996; Lazaro-Perea 2001; Raihani et al. 2010). Indeed, prospecting has been shown to be costly in meerkats, affecting both body mass and endocrine state (Young et al. 2005; Young and Monfort 2009). Studies on dispersal suggest that its timing is associated with body condition (reviewed in Dufty and Belthoff 2001), with dispersers being larger or in better condition than late or non-dispersers (e.g., O'Riain et al. 1996; Nunes et al. 1999; Barbraud et al. 2003), and a similar pattern may be expected for prospecting. Finally, indirect costs of prospecting may also influence the timing of forays. Reed et al. (1999) suggest that birds may prospect at the end of the breeding season in order to avoid compromising current breeding effort. In species with parental care, investment in prospecting may be timed according to the needs of dependent young, given the expected trade-off between providing care and seeking additional mating opportunities (Westneat et al. 1990; Magrath and Komdeur 2003). Such patterns

might also be expected among helpers in cooperative societies, as they too can face a comparable trade-off (Young et al. 2005).

### **1.1.2 Should subordinates prospect or help?**

In cooperatively breeding societies, subordinate individuals that delay dispersal and help raise offspring that are not their own can benefit from group augmentation (Kokko et al. 2001) and if helping kin, can also increase their indirect fitness (Hamilton 1964). Subordinates may also gain direct fitness benefits by prospecting, if it allows them to find mating or suitable dispersal opportunities during extraterritorial forays (e.g., Lazaro-Perea 2001; Young et al. 2007). As both helping and prospecting are expected to be costly and condition-dependent (Clutton-Brock et al. 2002, see above), levels of investment in either activity may respond to direct energetic and time allocation trade-offs between behaviours, as suggested for parental care and reproductive effort (Trivers 1972; Westneat et al. 1990). Indeed, recent studies on cooperative breeders suggest that subordinate individuals, trade off contributions to helping with current investment in prospecting (e.g., Young et al. 2005; Williams and Hale 2007). Along with the energetic and time allocation trade-offs, individuals may suffer alterations to their endocrine state while conducting prospecting forays, for example, as a result of aggressive interactions. In some cases, prospectors may return to their groups with altered levels of hormones, such as testosterone, that may affect the expression of parental care (Wingfield et al. 1990; Young et al. 2005). The level of investment in prospecting and helping may also be modulated by divergent life history strategies, as described for patterns of dispersal (e.g., O'Riain et al. 1996; Scantlebury et al. 2006), regardless of current levels of investment in either behaviour. As with dispersal, individuals experiencing favourable conditions in early life may invest more in prospecting later in life, if they are better able to cope with the cost of prospecting arising from extraterritorial movements and aggressive encounters with residents in neighbouring groups (Dufty and Belthoff 2001).

## **1.2 Overview of territory defence**

In many species, territories encompassing a series of limiting resources, such as food, shelter and mates, are exclusive and actively defended by residents against

conspecific intruders (Maher and Lott 1995). Territory defence typically involves the advertisement and maintenance of territorial boundaries through a suite of behaviours that may include scent marking, vocalizations and vigilance, and ultimately, chasing and fighting intruders (e.g., Krebs et al. 1978; Kacelnik et al. 1981; Gosling 1982; Packer et al. 1990; Lazaro-Perea 2001). These behaviours are expected to be costly, as they involve time, energy and, in some cases, risk to self (Davies 1980; Low 2006; Grinnell et al. 1995). Individuals typically trade off investment in other key behaviours such as foraging and parental care with territorial behaviours (Kacelnik et al. 1981; Wingfield et al. 1990), and injuries and death have been reported as a result of fighting during territorial encounters (e.g., Baker and Dietz 1996; Cant et al. 2002; Creel and Creel 2002). Thus, residents should only invest in territory defence when the benefits of territoriality outweigh the costs (Davies 1980). Keeping intruders excluded from a defined area may provide the benefit of a safe haven in which to breed (e.g., protection from infanticide; reviewed in Ebensperger 1998) and is expected to reduce direct intraspecific competition by giving territory holders priority of access to resources within the territory (Davies 1978; Kaufmann 1983). However, in group-living species, these benefits may not always be shared equally across members of a group (e.g., Boydston et al. 2001), which could lead to differences in individual contributions to repelling intruders.

### **1.2.1 Do all residents contribute to repelling intruders?**

Intruders vary in their motivation for trespassing into another individual or group's territory, yet they are frequently prospecting for breeding opportunities (Møller 1987) and may attempt to replace the resident breeder (e.g., Grinnell et al. 1995; Baker and Dietz 1996; Raihani et al. 2010). Consequently, intruders are typically in direct conflict with residents of their same sex (e.g., Møller 1987; Sillero-Zubiri et al. 1996). In societies with dominance hierarchies where access to mates within the group is skewed, differing levels of conflict with intruders may also exist between residents of the same sex. These differences in reproductive conflict with intruders can lead to divergent benefits of defending a territory, with dominant individuals standing to gain more than lower ranking individuals (Nunn 2000). Coupled with the costs of territoriality, skewed direct benefits may explain the individual differences in contributions to repelling intruders observed in many cooperative breeders (e.g.,



Baker and Dietz 1996; Cooney 2002). However, when offspring delay dispersal and help raise subsequent young in kin groups, indirect fitness benefits may also play an important role in modulating subordinates' investment in repelling intruders. By repelling intruders, subordinates may prevent copulations between residents and extra-group individuals, thereby ensuring that the primary breeders in the group are their parents and maximizing their own indirect fitness gains (e.g., mother guarding; Welbergen and Quader 2006). Furthermore, if subordinates are queuing for a breeding position within the group, any extra-group arrival could affect their position in the queue (Nunn 2000). Indeed, subordinate individuals contribute to territorial defence in a number of cooperative breeders (e.g., Wingfield and Lewis 1993; Baker and Dietz 1996; Lazaro-Perea 2001), and may even invest more than dominant breeders in repelling intruders (e.g., O'Riain and Jarvis 1997; Cant et al. 2002). Critically, contributions to territorial defence may not only involve repelling intruders through chasing and fighting, but also alerting other group-members of the presence of intruders once they are detected (e.g., O'Riain and Jarvis 1997; Manser 2001; Cant et al. 2002).

### **1.2.2 How do residents respond to intruder scent cues?**

In many mammal species, a potential way of detecting an intruder is through its scent (e.g., Hurst and Beynon 2004; O'Riain and Jarvis 1997). Communication by way of scent marks (i.e., urine, faeces and scent gland secretions), may allow individuals to convey information regarding their sex, identity, group membership, health and reproductive status (Johnson 1973; Wyatt 2003). In the context of territorial behaviours, scent marking is expected to allow residents to advertise territory ownership and their competitive abilities (Gosling 1982; Wyatt 2003; Hurst and Beynon 2004). Scent marking may also be used by intruders as a form of advertising their presence to potential mates and as a challenge to territory owners (Gosling and Roberts 2001; Hurst and Beynon 2004). Residents are expected to respond to these intruder scent marks more strongly than to those of their own group members, in ways that reflect the response to the intruders themselves. In cooperative breeders, however, the distribution of reproduction within groups may modulate the type of response to scent marks of extra-group individuals and the intensity, relative to the response to resident scent marks. In banded mongooses, for example, reproductive conflict within

the group may lead to sex-specific countermarking of group-member scent marks rather than those of intruders (e.g., Müller and Manser 2008; Jordan et al. 2011). In contrast, when there is high reproductive skew arising in large part from inbreeding avoidance within kin groups, breeding rivals are likely to come from outside the group, and thus strong responses would be expected toward intruder scent marks, particularly from dominant individuals. Nevertheless, all group members in cooperatively breeding societies may benefit from alerting others of the presence of an intruder, regardless of their level of reproductive conflict with extra-group individuals (O'Riain and Jarvis 1997), if the indirect benefits of territorial defence are considered (see above).

### **1.3 Thesis aims and structure**

In this dissertation, I use a combination of detailed behavioural observations, field experiments and approximately 12 years' worth of life-history data and body mass records, to investigate two broad questions: (i) what are the causes and consequences of individual variation in investment in prospecting behaviour by subordinate males, and (ii) what are the causes and consequences of individual variation in responses to prospectors by residents? My research focused on the cooperatively breeding meerkat, a diurnal species of mongoose that lives in groups of up to 50 individuals in the semiarid regions of southern Africa. The study population, located in the Kalahari desert in South Africa, has been studied for over 15 years and consists of individuals that are marked and habituated to the presence of observers, which allowed a unique opportunity to address my specific research aims, detailed below by chapter.

In Chapter 2, I give a general introduction to the study species, focusing on the population on which this study is based, and describe the general methods used throughout this dissertation.

In Chapter 3, I investigate the individual, social and environmental factors that affect the timing of extraterritorial prospecting forays by subordinate males, and assess whether meerkats maximize their probabilities of a successful foray by prospecting when there are ample mating and dispersal opportunities.

In Chapter 4, I investigate how investment in prospecting and helping behaviours in early life are affected by early-life body mass, and assess the evidence for potentially divergent developmental trajectories among subordinate males.

In Chapter 5, I investigate the extent of variation among resident individuals in their investment in repelling prospectors and quantify the benefits and costs of territorial behaviours, in order to assess how investment in these behaviours is modulated according to the cost and benefits of repelling intruders.

In Chapter 6, I first investigate whether meerkats are able to discriminate between resident and extra-group male scent cues, and second, investigate how sex and social status affects resident individuals' responses to the scent cues of extra-group males. I then investigate whether resident female reproductive status affects responses to extra-group male scent cues.

In Chapter 7, I synthesize the findings of this study and discuss their broader implications, offering suggestions for future work.



## CHAPTER 2

# General Methods

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### 2.1 Study site

This study was conducted at the Kuruman River Reserve (26° 59' S, 21° 50' E), a 35 km<sup>2</sup> expanse of former ranch land in the Kalahari desert, in the Northern Cape Province of South Africa (figure 2.1). The reserve was established in 1993 by Professor Tim Clutton-Brock to study cooperation in wild meerkats (Clutton-Brock et al. 1998b) and a team of researchers has been based there continuously since then, investigating a wide range of questions on the behavioural ecology of meerkats.



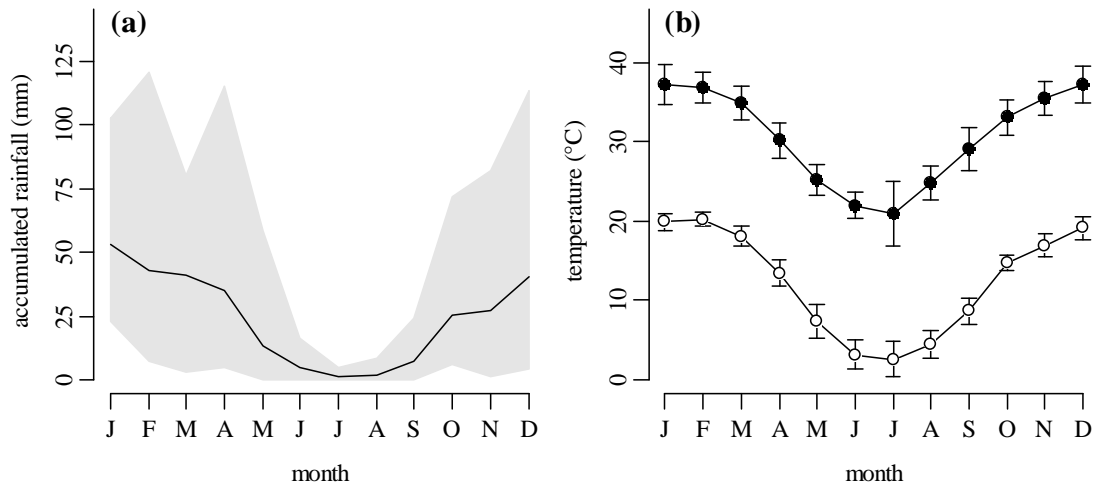
**Figure 2.1:** Location of the study site (star) within South Africa.

### 2.1.1 Habitat

The dry bed of the Kuruman River runs through the study site, with the rest of the habitat comprising typical Kalahari thornveld, flat lands interspersed with 10 – 30 m high sand dunes. The vegetation consists primarily of perennial and annual grasses (*Eragrostis* spp., *Aristida* spp., *Stipagrostis* spp. and *Schmidtia kalahariensis*) and perennial shrubs (*Rhigozum trichotomum* and *Grewia flava*), interspersed with isolated trees (*Acacia erioloba*, *Acacia mellifera* and *Boscia albitrunca*).

### 2.1.2 Climate

The study area has a semi-arid climate, characterized by low annual rainfall and extreme temperatures, with two distinct seasons: a cold, dry winter (May to September) and a hot, wet summer (October to April). Minimum and maximum temperatures (°C) at the study site were recorded daily, using an alcohol thermometer that was permanently suspended in the shade. Daily rainfall measurements (mm) were estimated for a 0.25° x 0.25° (latitude x longitude) area that encompassed the study site using the Tropical Rainfall Measuring Mission data set, which was accessed through the National Aeronautics and Space Administration's Goddard Earth Sciences Data and Information Services Center Interactive Online Visualization ANd aNalysis Infrastructure (Giovanni; <http://disc.sci.gsfc.nasa.gov/giovanni>). Figure 2.1 shows the monthly rainfall and temperature profiles for the study site.



**Figure 2.2:** (a) Monthly rainfall (mean, solid line; range, shaded area), and (b) minimum (open circles) and maximum (filled circles) temperatures (means  $\pm$  SD) at the Kuruman River Reserve, Northern Cape, South Africa, over a 12 year period (1998 – 2009).

### 2.1.3 Fauna

The Kuruman River Reserve's fauna includes native ungulate species, such as common eland, gemsbok, red hartebeest, springbok and blue wildebeest. All large terrestrial predators have been eliminated from the area by ranchers over the course of the past century, but smaller predators, including caracals, African wild cats and Cape foxes, are still present. There are also a number of aerial predators that prey on adult meerkats, such as steppe buzzards, black-breasted snake eagles, martial eagles and tawny eagles. Smaller raptors, such as lanner falcons, gabar goshawks and pale chanting goshawks, may also prey on pups but not adults. Pups are also likely to fall prey to venomous snakes (puff adders and Cape cobras) that have bitten and seriously injured or killed several adult meerkats, although no acts of predation have been reported.

## 2.2 Study species

Meerkats (*Suricata suricatta* Schreber, 1776), also known as suricates, are small (< 1 kg) desert-adapted carnivores that inhabit the semiarid regions of southern Africa, including Angola, Botswana, Namibia and South Africa. Meerkats are highly gregarious and live in groups of up to 50 individuals (Clutton-Brock et al. 2008).

They are members of the mongoose family (Herpestidae), which comprises 18 genera and 37 species (Veron et al. 2004) that include other well-studied gregarious mongooses, such as the banded mongoose (Rood 1974; Cant 2003) and dwarf mongoose (Rood 1978; Creel and Waser 1994).

### **2.2.1 Activity patterns and foraging behaviour**

Meerkats are diurnal, emerging from their overnight burrow at dawn (05:00 – 10:00 h) and spending up to an hour sunning, particularly in the colder months, before setting off as a group to forage. Groups forage as cohesive units, searching for and capturing prey individually. Meerkats feed primarily on subterranean invertebrates (e.g., beetle larvae, scorpions and millipedes) which they locate using olfaction and excavate using their forepaws, but also eat small vertebrates (small reptiles and rodents) and bulbs (Doolan and Macdonald 1996a; Brotherton et al. 2001). Groups typically forage for 3 – 4 h in the mornings and cease activities during the hottest hours of the day, particularly in the hotter months (e.g., December and January). Foraging resumes for 2 – 3 h in the afternoon until dusk (18:00 – 21:00 h), when groups return to overnight burrows and individuals engage in social behaviours, such as grooming, before going underground for the night (Kutsukake and Clutton-Brock 2006a). Meerkat groups use a series of overnight burrows scattered throughout their home ranges and typically switch between burrows once or twice a week, unless babysitting pups at a breeding burrow (Turbé 2006). Groups defend overlapping home ranges of approximately 2 km<sup>2</sup> against displacement from neighbouring groups through aggressive interactions (Young 2003; Jordan et al. 2007).

### **2.2.2 Social structure and reproduction**

Meerkats are obligate cooperative breeders, living in groups comprising a dominant pair and a variable number of subordinate males and females that delay dispersal. Dominant individuals monopolize reproduction, producing over 80% of the offspring in the group, whereas subordinates reproduce at a much lower rate than dominants and typically lack access to unrelated breeding partners in the group (Clutton-Brock et al. 1998a; O'Riain et al. 2000; Spong et al. 2008). Successful reproduction is heavily dependent on rainfall, with the majority of births occurring between October and April (Doolan and Macdonald 1997; Clutton-Brock et al. 1999b). Dominant females

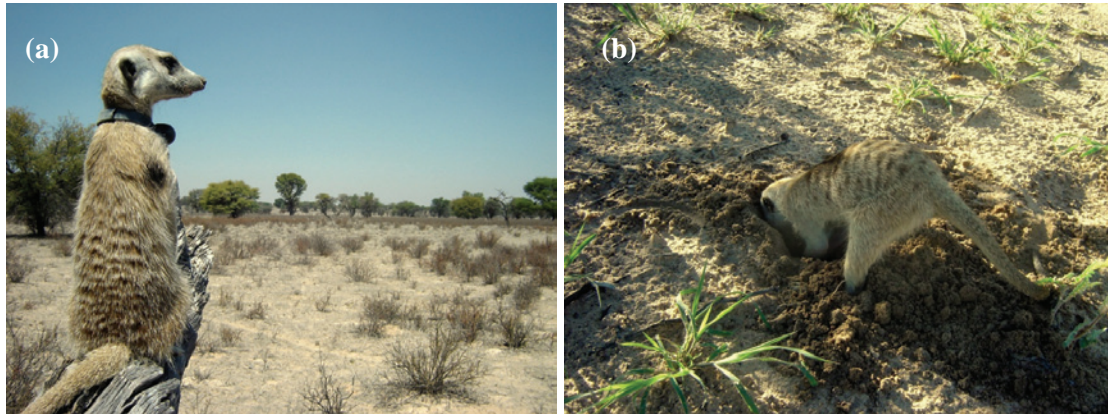


can produce up to four litters per year, with litter sizes ranging from one to seven pups. Pups spend their first three weeks below ground in a breeding burrow and begin to travel with the rest of the group when they are approximately 30 days old (Clutton-Brock et al. 1999b), but remain nutritionally dependent until they are approximately three months old (Brotherton et al. 2001). Individuals become sexually mature around one to two years of age, coinciding with the period during which subordinate males begin to disperse voluntarily and subordinate females are permanently evicted by the dominant female (Clutton-Brock et al. 2002). Males do not breed within their natal groups, but they are occasionally able to mate with extra-group females when on extraterritorial prospecting forays (Griffin et al. 2003; Young et al. 2007; Spong et al. 2008). Prospecting by subordinate males also allows subordinate females to breed, with extra-group copulations during prospecting forays accounting for a large proportion of subordinate reproduction (Young et al. 2007; Spong et al. 2008).

### **2.2.3 Cooperative behaviours**

Both female and male meerkats display a range of cooperative behaviours, such as the maintenance of burrow systems and raised guarding (Clutton-Brock et al. 2002). Raised guarding (i.e., vigilance from a raised position; figure 2.3a) is of particular importance when group members are foraging and most vulnerable to predators (figure 2.3b). Guards alert other group members if predators approach, thus allowing foraging individuals to be less vigilant (Manser 1998). Cooperative activities also include caring of young, specifically, babysitting and pup feeding (Doolan and Macdonald 1999). Babysitting involves one or more group members remaining at the breeding burrow for up to a full day with pups that are too young (approximately 0 – 30 days of age) to forage with the rest of the group. Pup feeding involves provisioning food to young that have started to travel with the group, but have not yet developed the skills to forage for themselves (approximately 30 – 90 days of age). Individuals begin contributing to these cooperative activities after nutritional independence (approximately three months of age), but contributions to each activity may vary between group members depending on their age, body mass, sex and social status (Clutton-Brock et al. 1998b; Clutton-Brock et al. 1999c; Clutton-Brock et al. 2002). Group members may also cooperate in territorial defence by contributing to the

repulsion of neighbouring groups (Young 2003; Jordan et al. 2007) or prospecting males, yet these behaviours have received considerably less attention.



**Figure 2.3:** A meerkat on raised guard (a) and a meerkat digging for prey (b).

#### 2.2.4 Communication

Meerkats use both vocal and olfactory signals to communicate within and between groups. Vocalizations are used to maintain group cohesion and coordinate group movement when meerkat groups are foraging (Manser 1998). A large repertoire of alarm-like vocalizations is also used to indicate the presence and type of predators, the presence of neighbouring groups, as well as the secondary cues of both predators and foreign groups (Manser et al. 2001). Olfactory cues, deposited as scent marks, advertise territory ownership, are likely to play a role in mate defence and may allow group members to monitor the reproductive status of resident and extra-group females (Jordan et al. 2007; Jordan 2007). Scent marking in meerkats involves anal marking (wiping the anal region across a surface), chew marking (biting vegetation), scuffing (frenzied digging), urinating and defecating (Jordan 2007). These scent marks are typically deposited at latrines (Jordan et al. 2007), but are also deposited individually at conspicuous locations, such as around overnight burrows. Dominant males also typically place anal marks on other group members.

## **2.3 Study population**

This study involved a combination of analyses of the long-term database and my own behavioural observations and experiments. I included life history and behavioural data collected continuously between 1998 and 2009 by teams of 4 – 10 volunteer field assistants working at the Kuruman River Reserve. My own behavioural observations and experiments were conducted during two field seasons: August 2008 – February 2009 and August 2009 – February 2010. In each of the 12 years (1998 – 2009) on which my study focuses, 13 – 21 groups ranging in size from 3 – 50 individuals were monitored. All research protocols were approved by the Research Ethics Committee at the University of Cambridge and permission to conduct research was granted by the Northern Cape Conservation Service, South Africa.

### **2.3.1 Habituation and individual identification**

All meerkats in the study population were habituated to close observation (< 1 m), which made it possible to collect detailed behavioural data and conduct experiments. For identification purposes, individuals were implanted soon after birth with a small subcutaneous transponder chip, each with a unique code (Clutton-Brock et al. 2001a). In addition, unique combinations of dye-marks were applied on the fur of each meerkat, to allow rapid identification during field observations (Jordan et al. 2007).

## **2.4 Data collection**

All study groups were visited once every three days to assess group size, composition and the pregnancy status of females. Groups were located by radio-tracking, as at least one adult individual in each group was fitted with a VHF radio collar (Sirtrack, New Zealand). Details on the capturing methods used to fit animals with radio collars are described by Jordan et al. (2007). Collared individuals could be tracked from a distance of up to 1.5 km using a directional antenna (Telonics, USA) attached to a telemetry receiver (R-1000, Communications Specialists, USA).

### 2.4.1 Life history data

*Reproduction.* Pregnancy lasts for approximately 70 days (Clutton-Brock et al. 2008) and was determined by a swelling of the abdomen and increase in weight from the fourth week after conception. Births or abortions could be determined by a sudden decrease in weight and change in body shape. After a litter was born, groups were visited more frequently to record the identity of babysitters until pups began travelling with the rest of the group. Females typically experience a brief (approximately three days), post-partum oestrus and were also assumed to be in oestrus whenever dominant males were observed mate-guarding them (Jordan et al. 2007) or if seen mating.

*Age categorization.* Unless otherwise stated, age was categorised as follows: < 91 days (pup), 91 – 180 days (juvenile), 181 – 360 days (subadult) and > 360 days (adult). As groups were visited three to four days a week during the breeding season, the birth dates for most individuals were known to an accuracy of three days. ‘Group size’ refers to the number of individuals more than 90 days of age in the group on a given day, as pups do not contribute to cooperative activities (Clutton-Brock et al. 2002) and are nutritionally dependent on older group members (Brotherton et al. 2001).

*Social status.* Within each group, one male and one female were clearly behaviourally dominant to all other same-sex individuals. Dominant individuals are typically the oldest and the primary breeders in their groups (Griffin et al. 2003; Spong et al. 2008), and are frequently aggressive to subordinates of their sex, who generally respond with submissive behaviours (O’Riain et al. 2000; Kutsukake and Clutton-Brock 2006b; Kutsukake and Clutton-Brock 2008). Subordinates are also known as helpers and comprise all group members (excluding dominants) more than 90 days of age.

### 2.4.2 Weight data

Meerkats were trained from an early age to stand on a top-pan electronic balance (Talent TE4100, Sartorius, UK) in return for a small reward of hard-boiled egg crumbs or water from a hamster water bottle (figure 2.4). Most individuals (> 90%) could thus be weighed to an accuracy of 1 g throughout their lives. Individuals were typically weighed three times a day: at dawn before groups began foraging (morning weight); 2 – 4 h later at the end of a morning observation session (lunch weight); and

in the evening prior to going below ground (evening weight). Rates of weight gain (g/h) were estimated by subtracting an individual's morning weight from its lunch weight, and dividing the difference by the number of hours elapsed between weight measurements. Throughout this dissertation, I use an individual's morning weight as its measure of body mass, as weights recorded in the morning exhibit the least daily variation.



**Figure 2.4:** A meerkat being rewarded with water after stepping on the scales.

### 2.4.3 Behavioural data

Unless otherwise stated, behavioural data were recorded *ad libitum* during visits to groups either in the morning, lasting 2 – 4 h from the time when groups started foraging; or in the afternoon, lasting 1 – 2 h before the group returned to an overnight burrow. All behavioural data were recorded on a handheld computer (Organiser II LZ64, Psion Teklogix, UK) with times accurate to 1 s. I also collected behavioural data by conducting focal observations (Altmann 1974) of specific individuals. Full details of the focal observation methods are given in the relevant chapters.

### 2.4.4 Experimental data

In addition to collecting observational data, I conducted a series of experiments where individuals were presented with faecal samples. Full details of the experimental protocols and sample collection methods are given in the relevant chapter.

## 2.5 Statistical analyses

All analyses were conducted using R (R Development Core Team 2011), a free software environment for statistical computing, with add-on packages for the specific statistical methods used (detailed in the relevant chapters). In general, my analyses required the use of multivariate statistical methods, such as linear mixed models (LMM), given that datasets included repeated measures of individuals or groups. Mixed models allow both fixed terms (e.g., age), that influence the mean of a response, and random terms (e.g., individual), that influence the variance, to be fitted (Crawley 2007). When models included more than one random term, such as individual and group, these could be nested or crossed according to the structure of the data: for example, if individuals changed groups the two random effects were crossed, otherwise, individuals were nested within groups. Model error structures (e.g., Gaussian or binomial) were determined based on the distribution of the response variable and are detailed in the relevant chapters.

For analyses of observational data collected in non-experimental settings, I used an information-theoretic approach (see Burnham and Anderson 2002). Following this approach, a set of candidate models were described using variable combinations of predictors of interest. These models were fitted to the data, and ranked according to their predictive ability, as assessed by Akaike's information criterion values (AIC; Akaike 1973), or a corrected form of AIC (AICc) when the ratio of the sample size to the parameters estimated was small ( $< 40$ ; Burnham and Anderson 2002). Differences in AIC ( $\Delta_i$ , a model's AIC minus the minimum AIC among candidate models) were calculated for each model and those with  $\Delta_i$  less than two were considered to be the 'best', opting for simpler models (those with fewer estimated parameters) when more than one model had  $\Delta_i < 2$  and similar fits to the data in terms of log-likelihood (Burnham and Anderson 2002). Further details on the methods involved in building candidate model sets are presented in the relevant chapters.

For analyses of experimental data, I used a hypothesis-testing approach (Burnham and Anderson 2002; Crawley 2007). A stepwise selection method was used in which initial models included all potential explanatory variables and their interactions (Crawley 2007). Fixed terms were then dropped from the initial model in order of significance using a likelihood ratio test which compared the deviance of models with and without the term of interest. Fixed terms were removed until a

minimal adequate model was achieved in which the removal of any terms significantly decreased the fit of the model. Levels of significance and non-significance reported for all fixed terms were obtained by comparing minimal adequate models with models in which the term of interest had been added (for non-significant terms) or removed (for significant terms).





**CHAPTER 3****Timing and duration of extraterritorial prospecting forays by subordinate males**

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**3.1 Abstract**

In social species with high reproductive skew, extraterritorial prospecting may allow subordinate individuals to assess dispersal opportunities and breed while still in the natal group. Such prospecting may be costly, and forays may therefore be timed to maximize the probabilities of acquiring information on dispersal opportunities and of mating with extra-group individuals. Individuals may also attempt to minimize their long-term costs by modulating their investment in prospecting forays according to their current state. In spite of these predictions, the causes of individual variation in investment in prospecting behaviour and the proximate factors influencing its timing have rarely been explored. Here, I investigate the factors influencing the timing and

duration of prospecting forays by subordinate male meerkats. I found that the timing of prospecting forays followed a consistent seasonal pattern that coincided with periods of low accumulated rainfall, high female fertility and patterns of subordinate female evictions, but was not predicted solely by any of these terms. I also found that males were more likely to prospect on weeks when their groups were involved in an intergroup interaction and when the number of evicted females in the population (potential companions for the founding of new groups) was high. Older and heavier males were also more likely to prospect throughout the prospecting season. Finally, I found that males were more likely to return to their own groups on the same day as they departed when their group was involved in an intergroup interaction (when their destination group was close to their own group) or babysitting (when their own group could easily be located upon returning). My results reveal that patterns of prospecting by subordinate males are highly seasonal and cannot be predicted solely by patterns of fertility or potential dispersal opportunities, but investment in prospecting is influenced by the proximity between groups, the availability of dispersal opportunities and the costs associated with prospecting.

### **3.2 Introduction**

Prospecting behaviour has been considered primarily as a means of gathering information on future dispersal and breeding sites (reviewed in Reed et al. 1999; Danchin et al. 2001), but temporary extraterritorial forays may additionally enable access to mating opportunities in a number of species (birds: Westneat and Stewart 2003; mammals: Waser 1996). In ‘high skew’ social species, where within-group reproduction is monopolised by a small number of dominant individuals, prospecting forays may be the primary route to reproduction for subordinate group members (e.g., Lazaro-Perea 2001; Young et al. 2007). The ability to assess dispersal opportunities and gain access to extra-group copulations during extraterritorial forays, while still resident within the natal group, may ultimately minimize the costs of delaying dispersal, in terms of lost reproduction (Kokko and Ekman 2002). Remarkably few studies, however, have investigated the causes of individual variation in investment in prospecting behaviour and the proximate factors influencing its timing (Danchin et al. 2001). This is perhaps surprising, given the importance of considering individual

variation in dispersal and extra-group mating behaviour for understanding population genetics and dynamics (Clobert et al. 2009; Cote et al. 2010), as well as the evolution of cooperation (Kokko and Ekman 2002; Hatchwell 2009).

Prospecting is likely to be a costly activity (Danchin et al. 2001), and individuals are expected to attempt to mitigate the potential costs by timing their forays appropriately, using social (Reed et al. 1999) or environmental cues (Bowler and Benton 2005), or by prospecting in a state-dependent manner (Dufty and Belthoff 2001). Extraterritorial forays typically involve travelling alone (or in reduced numbers) and in unfamiliar areas, both of which can increase the risk of predation and have detrimental effects on condition (Waser 1996; Dufty and Belthoff 2001). In addition to bearing similar costs to those associated with dispersal movements (Bowler and Benton 2005), prospectors may face the challenge of finding their own group upon returning from an extraterritorial foray. A range of studies have now found that prospectors may experience loss of body condition, chronically elevated stress levels and aggression from foreign individuals (e.g., Lazaro-Perea 2001; Young et al. 2005; Young and Monfort 2009; Raihani et al. 2010; Chapter 5). Given these potentially high costs, one might predict that subordinate individuals, first, prospect at times that maximize their chances of both encountering extra-group mating opportunities and gathering information regarding future dispersal opportunities; and, second, modulate their investment in prospecting forays so as to minimize their long-term costs, for example, by prospecting in a condition-dependent manner as frequently occurs with dispersal (Dufty and Belthoff 2001).

Here, I investigate the factors that influence the timing and duration of extraterritorial prospecting forays by subordinate males in the cooperatively breeding meerkat. Meerkats live in groups of up to 50 individuals, where a single, typically unrelated, dominant pair largely monopolizes within-group reproduction and close inbreeding is avoided (Griffin et al. 2003; Spong et al. 2008). Dispersal is delayed beyond the age of sexual maturity in both males and females, who remain in their natal groups as subordinate helpers (Clutton-Brock et al. 2002; Russell et al. 2007). Both sexes may ultimately disperse, but while subordinate females are evicted by the dominant female during her pregnancy (Clutton-Brock et al. 1998a), males conduct extraterritorial prospecting forays throughout the breeding season, with no evidence of increased levels of aggression preceding their departure (Young et al. 2007).

Prospecting males regularly approach foreign groups and attempt to mate with both dominant and subordinate females, which may yield the majority of subordinate male reproductive success and can lead to appreciable levels of extra-group paternity (Young et al. 2007; Spong et al. 2008). Ultimately, extra-group males may take over an established breeding group or, alternatively, form a new group by joining a coalition of evicted females (Doolan and Macdonald 1996b; Young 2003; Clutton-Brock et al. 2008; Chapter 5). Prospecting is not without its costs, however: individuals are expected to experience higher predation risk while travelling away from their groups (Clutton-Brock et al. 1999a) and previous studies have shown that prospectors suffer from condition loss and elevated physiological stress levels (Young et al. 2005; Young and Monfort 2009). In addition, upon approaching foreign groups, prospectors are aggressively chased by resident individuals which can lead to serious injuries or even death (Doolan and Macdonald 1996b; Young 2003; Chapter 5).

Given the high risks associated with prospecting in meerkats, males would be expected to time their forays when extra-group mating opportunities are most abundant and when the assessment of dispersal opportunities is most feasible. Furthermore, heavier males may be able to invest more in prospecting and may do so primarily when the costs of prospecting are potentially lower, for example, when their own group is close to a neighbouring group or after recent rainfall, when food availability is high (Cumming and Bernard 1997). Previous studies have shown that prospectors tend to visit neighbouring groups (Drewe et al. 2009), spend more time prospecting during months when female fertility is high (Young et al. 2007) and that decreases in body mass while prospecting are correlated with the amount of time spent on forays (Young et al. 2005). However, it is unknown specifically what factors influence investment in these forays, and whether the timing of prospecting is correlated with indicators of extra-group mating and dispersal opportunities from within the prospector's own group or principally from seasonal variation that may encompass both patterns of mating and dispersal opportunities. It is also unknown whether the duration and, thus, likely costs of prospecting forays are influenced by the proximity of neighbouring groups to the prospector's own group and the likelihood that prospectors will find their own groups when attempting to return from extraterritorial forays. In this study, I use an 11 year data set to explore the causes of variation in investment in prospecting by subordinate males. Specifically, I investigate

the extent to which prospecting decisions are modulated according to a suite of factors that are likely to affect the benefits and costs of forays: temporal patterns of rainfall, female fertility and eviction within the prospector's own group and across the population, encounters between groups, and male age and body mass. I then investigate the causes of variation in the duration of forays, to explore whether subordinate males mitigate the costs of prospecting by modulating the duration of their forays according to age and body mass.

### **3.3 Methods**

#### **3.3.1 Study population**

The study was conducted using data collected from 1999 to 2009 on a wild population of meerkats at the Kuruman River Reserve (26° 59' S, 21° 50' E) and surrounding ranch land in the southern Kalahari desert, South Africa. The study population consisted of 13 to 21 groups in any given year, and all individuals were identifiable by unique dye marks on their fur and were habituated to close observation (within 2 m). Groups were visited at least once every three days and life history events for each individual, including dates of birth, reproduction and emigration, were generally known to the day. Subordinate males that were temporarily absent from the group, with no prior signs of illness, were considered to be prospecting. My study focuses on adult (> 360 days of age) subordinate males that were residing in their natal groups and of up to three years of age, as most males dispersed after their third year. After dispersing, males are typically able to mate with females in their new group and reduce their investment in prospecting (Young et al. 2007). Over the 11 year study period, 4013 prospecting forays were recorded for 362 subordinate natal males from 15 groups, with approximately 40% of the forays confirmed by observations of the absent male approaching another group.

#### **3.3.2 General statistical methods**

All statistical analyses were conducted using R (version 2.14; R Development Core Team 2011) with lme4 (version 0.999375-42; Bates et al. 2011) for building generalized linear mixed models (GLMM). Model selection and comparison (see

details below) were achieved using Akaike's information criterion values (AIC; Akaike 1973). I calculated AIC differences ( $\Delta_i$ , the model's AIC minus the minimum AIC among candidate models) for each model and considered those with  $\Delta_i$  less than two to be the 'best' (Burnham and Anderson 2002). I standardized continuous input variables by subtracting the mean and dividing by two standard deviations (SD), to allow the comparison of their estimated effect sizes with those of binary predictors and facilitate the interpretation of interactions (Gelman and Hill 2007; Schielzeth 2010).

### 3.3.3 Timing of prospecting forays

I investigated the relative importance of the potential predictors of investment in and timing of extraterritorial prospecting forays using GLMMs and data for 362 subordinate natal males. Using the dates on which subordinate males departed from their groups on prospecting forays ( $n = 4013$  departure dates), I determined that departures were never observed to occur in early April and, therefore, considered mid-April as the earliest possible start of a prospecting season (figure 3.1a). In order to facilitate the inclusion of a quadratic seasonal predictor of prospecting forays in the models (see below; table 3.1), I divided each calendar year of data into 52 weeks starting in mid-April and ending in April of the following year. I then determined, for each subordinate male, whether or not he had departed from his group on a prospecting foray in each week on which he was observed ( $n = 18631$  male weeks), and used these binary data as the response variable in a set of GLMMs with binomial error structure and logit link function. Each of six candidate models included one of the following highly seasonal and correlated predictors: (1) week within the prospecting season (as a continuous quadratic term; range 1 – 52); (2) total rainfall during the month before the start of the week (figure 3.1b); (3) mean probability of dominant female oestrus during the week, across the population (figure 3.1c); (4) average number of evicted females per group during the week, across the population (figure 3.1d); (5) whether or not the dominant female was likely to be in oestrus (probability > 0.05) during the week, within each male's group; and (6) average number of evicted subordinate females during the week, within each male's group. A further five models were constructed, which included both week and a relative measure, adjusted for week, of one of the other five variables detailed above (rain,

and population- and group-level oestrus and eviction patterns). Relative measures (termed ‘week-corrected’) were attained by subtracting the mean across all years for a given week from each value, and were used for these additional seasonal variables in order to account for their correlation with week. Individual identity was fitted as the random term in all of the candidate models in the set (table 3.1), which also included the following input variables and their two-way interactions with the unmodified seasonal predictor included in each model: male age and age-corrected body mass at the start of each week, and whether or not the male’s group was involved in an intergroup interaction during the week.

### **3.3.4 Duration of prospecting forays**

I used data from 2304 prospecting forays ( $n = 271$  subordinate males) to determine the factors that influence the duration of prospecting forays. For this analysis, I only included prospecting forays that coincided with the presence of an observer at the prospector’s group on the day of departure and the following morning, excluding cases where it was unknown if the prospector returned on the same day of departure or not. On 73% of these forays, prospectors returned to their groups on the same day, with duration of the remaining forays ranging between 1 and 22 nights away from the group (median = 1 night). Given the dispersed distribution of these foray durations, I fitted whether or not a prospector returned to his own group on the day of departure as a binary response variable, rather than the absolute duration, in a set of GLMMs with binomial error structure and logit link function. Individual identity was fitted as the random term in all of the candidate models (table 3.3), which also included different combinations of the following input variables measured on the day that prospectors departed from their own group: prospector age and age-corrected body mass, total rainfall in the previous month, whether or not the prospector’s group was involved in an intergroup interaction and whether or not his group was babysitting. The occurrence of an intergroup interaction was included as a proxy for proximity between a prospector’s group and his likely destination (i.e., the neighbouring group encountered). Whether or not the prospector’s group was babysitting, was included as a proxy for overnight burrow use consistency (i.e., same burrow on morning and evening of departure), and thus, the likelihood that prospectors would be able to find their own groups when returning from extraterritorial forays.

### 3.3.5 Data collection and definition of terms

*Female fertility patterns.* To estimate fertility patterns across the study groups, as an indicator of mating opportunity abundance, I compiled a data set of oestrus timings of dominant females. I focused exclusively on oestrus in dominant females, as subordinate female reproduction is unlikely to reflect seasonal variation in fertility accurately, given that they typically lack access to breeding partners (Young et al. 2007; Griffin et al. 2003). I combined information on cases of observed behavioural oestrus ( $n = 158$  observations), with those that otherwise had to be estimated using dates of birth, abortion and first detection of pregnancy. Dominant females were considered to be in oestrus when they were observed either mating or being mate guarded by the dominant male (Jordan et al. 2007). I estimated 349 oestrus periods by calculating (a) a probability distribution for the duration of oestrus ( $\bar{x} = 3.7$  days, range 1 – 11;  $n = 87$  observations of complete behavioural oestrus periods); and (b) the lag between birth or abortion and the onset of postpartum oestrus ( $\bar{x} = 6.3$  days, range 2 – 15;  $n = 40$  observations). For associated births ( $n = 280$  oestrus periods), I also estimated (c) the interval between observed onset of oestrus and subsequent birth ( $\bar{x} = 75.5$  days, range 65 – 75;  $n = 73$  observations); and for abortions ( $n = 69$  oestrus periods), (d) the interval between the onset of oestrus and subsequent detection of pregnancy ( $\bar{x} = 38.4$  days, range 17 – 67;  $n = 67$  observations), and the interval between detection of pregnancy and abortion ( $\bar{x} = 16.4$  days, range 0 – 60 days;  $n = 146$  observations). The probability distribution of the duration of oestrus (a) was then added to the probability of the onset of oestrus for each day leading to a reproductive event (birth or abortion), given an interval between reproductive events and the parameters estimated above for births (b, c) or abortions (b, d).

*Eviction patterns.* I estimated eviction patterns across the study groups, as an indicator of the availability of dispersal opportunities, by counting all days when subordinate females were absent from their group due to eviction. Subordinate females typically attempt to return to their groups after being chased aggressively by the dominant female, but evicted females have been observed associating temporarily with prospecting males, which can ultimately lead to dispersal and the founding of new groups (Clutton-Brock et al. 2008). A conservative approach was taken to considering temporary departures by subordinate females from their groups as cases of eviction,



by using only cases when aggression by the dominant female was observed prior to a subordinate female's departure ( $n = 525$  evictions).

*Age-corrected body mass.* Individuals in the population were trained to step on an electronic balance for small rewards of water or crumbs of hard boiled egg, which allowed the recording of body mass (to an accuracy of 1 g) before individuals started foraging in the mornings. To obtain a male's age-corrected body mass, I first calculated a predicted mass at each age in days for each male included in the analyses. I used predicted measures of body mass instead of actual mass records, as mass records obtained in the field were not available for every day for every individual. Predicted body mass was obtained from a biphasic growth model (English et al. 2011), using morning body mass records from 1064 males and females ( $n = 280260$  records of body mass), excluding measurements from females in the latter stages of pregnancy ( $< 40$  days to parturition or abortion; S. Sharp and T. Clutton-Brock, unpublished manuscript). I then subtracted the mean predicted mass across all individuals for a given age from a male's predicted body mass at the same age, in order to obtain an age-corrected body mass.

*Monthly rainfall.* I used monthly measures of rainfall in my analyses as a proxy for food availability (Cumming and Bernard 1997; Doolan and Macdonald 1997). Monthly rainfall was estimated using daily measures obtained from the Tropical Rainfall Measuring Mission data set, using the National Aeronautics and Space Administration's Goddard Earth Sciences Data and Information Services Center Interactive Online Visualization ANd aNalysis Infrastructure (Giovanni; <http://disc.sci.gsfc.nasa.gov/giovanni>).

*Intergroup interactions.* Interactions typically occur between neighbouring groups and involve aggressive behaviours, such as 'war-dancing', chasing and fighting, between groups (Jordan et al. 2007; Drewe et al. 2009), but subordinate males have also been observed trailing the encountered group after an interaction. Over the course of the study period, a total of 960 intergroup interactions were recorded for the 15 study groups. I used whether or not a group was involved in an intergroup interaction, as a proxy for the proximity between neighbouring groups.

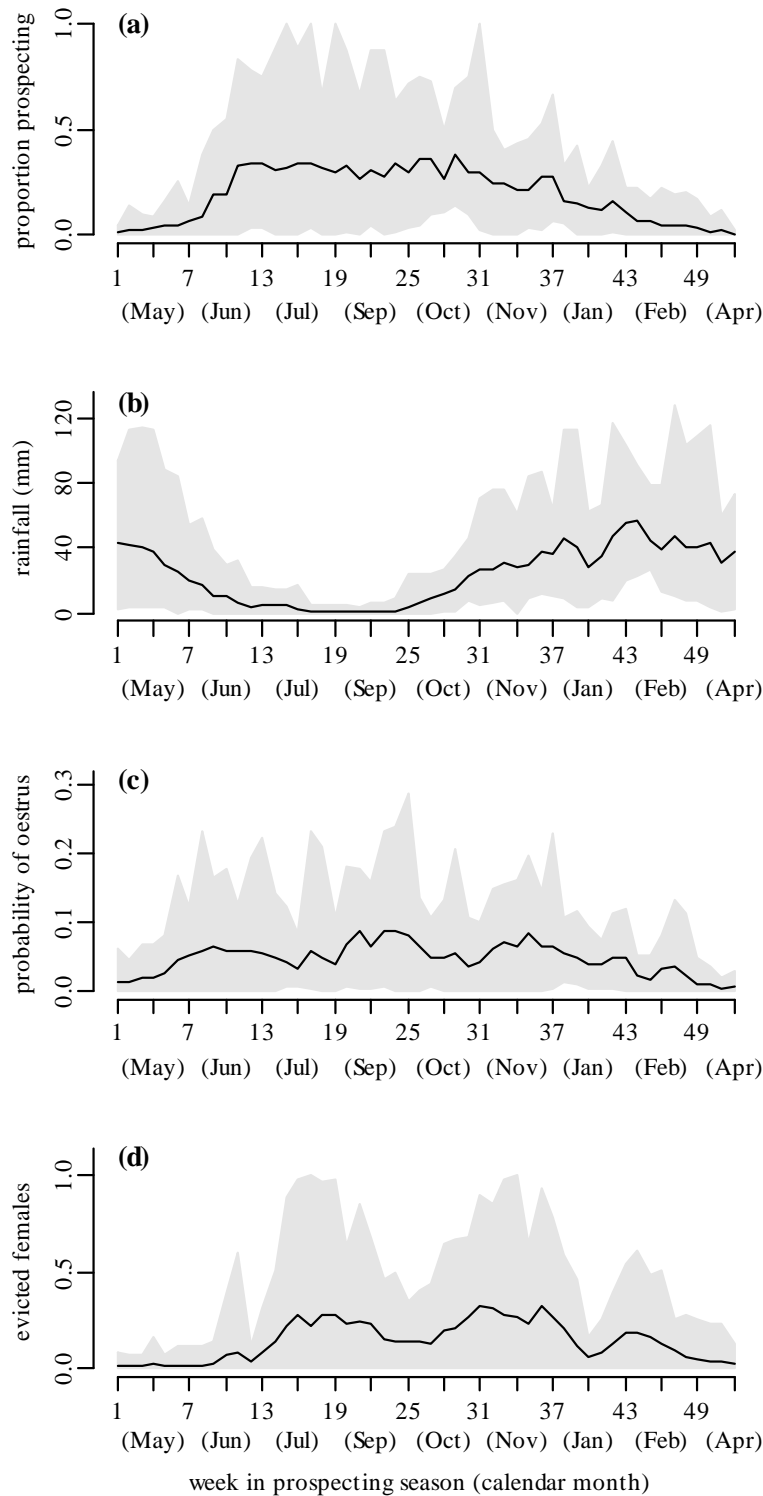
*Overnight burrow use.* Meerkat groups typically switch between approximately 20 overnight burrows scattered across their territories every three to four days, unless

they are babysitting young, in which case they consistently use a single breeding burrow (Clutton-Brock et al. 2000; Turbé 2006; Jordan et al. 2007). Babysitting spans the whole period from the birth of a litter until the litter starts foraging with the group or until the litter is abandoned or lost before foraging with the group ( $\bar{x}$  = 28.2 days, range 8 – 48). I used whether or not a group was babysitting, as a proxy for consistency in overnight burrow use.

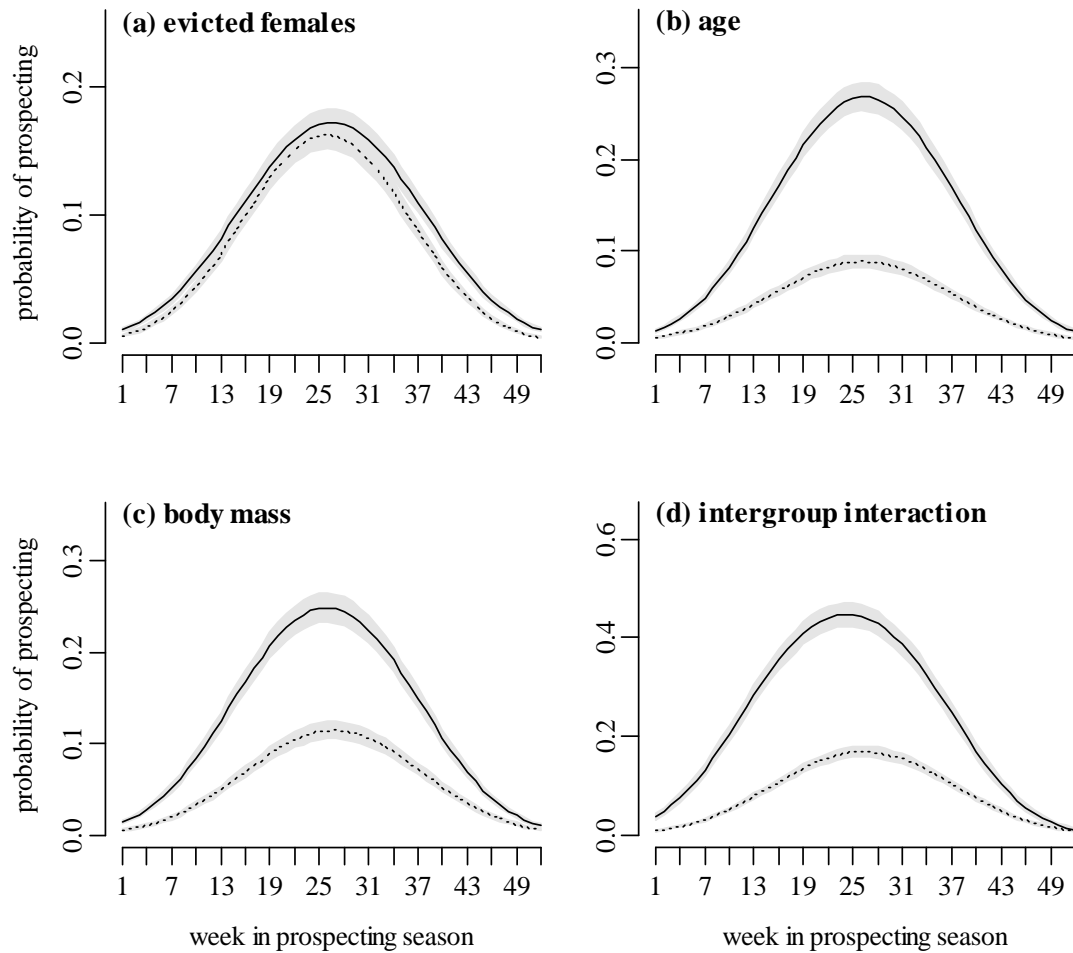
## 3.4 Results

### 3.4.1 Timing of prospecting forays

Subordinate natal males mainly conducted prospecting forays from June until January of the following year, spanning the weeks for which accumulated monthly rainfall was low, and dominant female fertility and numbers of evicted females were high across the population (figure 3.1). Among candidate models with a single seasonal predictor (bottom six in table 3.1), the best model of the probability of prospecting in each week included week of the prospecting season, suggesting that a simple quadratic function of week was a better predictor of prospecting than accumulated rainfall, or population- and group-level patterns of dominant female fertility and subordinate female eviction. Incorporating week-corrected values of these seasonal predictors, however, improved the fit of the basic model including week alone. The best overall model included the week-corrected number of evicted subordinate females across the population (table 3.1), which was positively correlated with the probability of prospecting (figure 3.2a; table 3.2). A subordinate male's age and age-corrected body mass at the start of the week were also positively correlated with the probability of prospecting, as was the occurrence of an intergroup interaction during the week. The estimated effects of age, age-corrected body mass, intergroup interactions and week-corrected number of evicted females across the population were greatest on weeks when prospecting levels were expected to be high (figures 3.2b-d), owing to the considerable effects of the two-way interactions between these terms and the quadratic function of week (table 3.2).



**Figure 3.1:** Means (solid lines) and ranges (shaded areas) of weekly measures of (a) proportion of subordinate males that prospecting ( $n = 362$  males), (b) total rainfall in previous month, (c) probability of dominant female oestrus per group per day and (d) number of evicted subordinate females per group per day, estimated using data collected from 1999 – 2009.



**Figure 3.2:** Effects on the probability of prospecting of the two-way interactions between week in the prospecting season and low (dotted lines) and high (solid lines) values for (a) week-corrected number of evicted females across the population, a prospector's (b) age and (c) age-corrected body mass at the start of the week, and (d) whether or not the prospector's group was involved in an intergroup interaction during the week. Predictions were estimated from the GLMM in table 3.2, setting the predictors not graphed to the mean, and using the first and third quartiles (low: dotted lines, high: solid lines, respectively) of the predictors plotted in (a), (b) and (c), and 0 and 1 (no: dotted line, yes: solid line) for (d). Shaded areas are prediction intervals (SE) accounting for the uncertainty in the estimates of the fixed effects.

Fixed terms	$\log(L)$	d.f.	AIC	$\Delta_i$
$(A + M + I + cEp) * (W + W^2)$	-5719.59	16	11471.18	0.00
$(A + M + I + cOp) * (W + W^2)$	-5739.25	16	11510.50	39.32
$(A + M + I + cR) * (W + W^2)$	-5761.15	16	11554.30	83.12
$(A + M + I + cEg) * (W + W^2)$	-5766.02	16	11564.04	92.86
$(A + M + I + cOg) * (W + W^2)$	-5767.59	16	11567.18	95.99
$(A + M + I) * (W + W^2)$	-5776.71	13	11579.41	108.23
$(A + M + I) * Ep$	-6222.21	9	12462.42	991.24
$(A + M + I) * R$	-6324.40	9	12666.80	1195.62
$(A + M + I) * Op$	-6334.35	9	12686.69	1215.51
$(A + M + I) * Eg$	-6389.50	9	12797.00	1325.81
$(A + M + I) * Og$	-6438.39	9	12894.78	1423.60

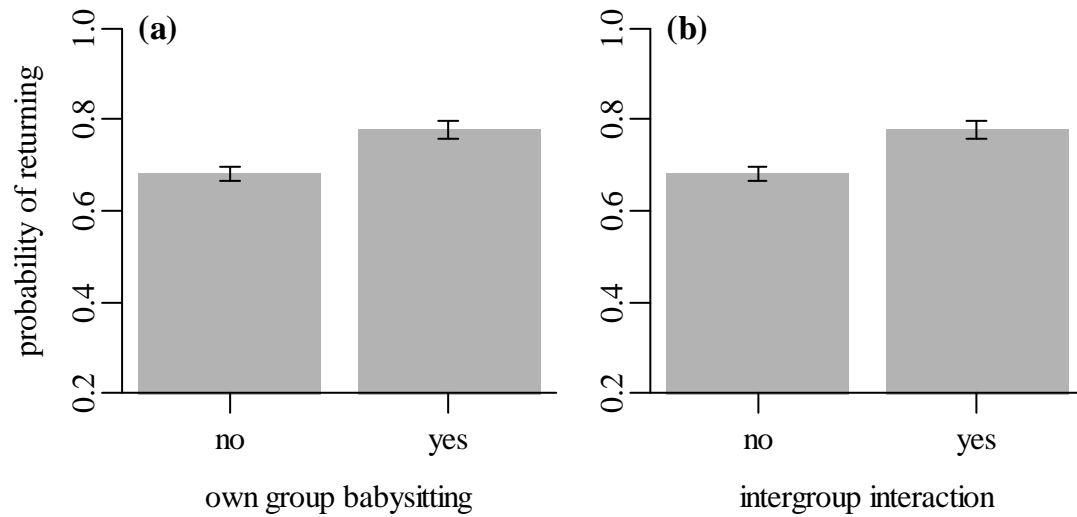
**Table 3.1:** Candidate models for the factors influencing the timing of prospecting forays by subordinate males. For all models: A = age; M = age-corrected body mass; I = intergroup interaction; W = week of prospecting season; R = total rainfall in previous month; O = probability of dominant female oestrus; E = number of evicted subordinate females; p = across population; g = within groups; c = week-corrected. All GLMMs were fitted with whether or not a male prospected on a given week ( $n = 18631$  male weeks) as the binary response variable and included individual identity ( $n = 362$  males) as a random term.

Fixed terms	Estimate $\pm$ SE	$z$	$P$
(Intercept)	-1.60 $\pm$ 0.08	-20.41	
Age	1.79 $\pm$ 0.08	22.89	
Body mass <sup>a</sup>	1.33 $\pm$ 0.13	10.46	
Intergroup interaction (yes)	1.37 $\pm$ 0.08	16.57	
Evicted females <sup>b</sup>	0.46 $\pm$ 0.18	2.65	
Week	0.18 $\pm$ 0.09	2.11	
Week <sup>2</sup>	-4.79 $\pm$ 0.20	-23.46	
Age * Week	0.14 $\pm$ 0.13	1.09	0.274
Age * Week <sup>2</sup>	-0.85 $\pm$ 0.31	-2.72	0.006
Body mass <sup>a</sup> * Week	-0.36 $\pm$ 0.14	-2.54	0.011
Body mass <sup>a</sup> * Week <sup>2</sup>	-0.37 $\pm$ 0.33	-1.10	0.273
Intergroup interaction * Week	-0.67 $\pm$ 0.15	-4.61	< 0.001
Intergroup interaction * Week <sup>2</sup>	-0.63 $\pm$ 0.35	-1.80	0.072
Evicted females <sup>b</sup> * Week	1.08 $\pm$ 0.46	2.34	0.019
Evicted females <sup>b</sup> * Week <sup>2</sup>	7.31 $\pm$ 1.32	5.53	< 0.001

**Table 3.2:** Factors affecting the timing of prospecting forays by subordinate males. Results from the best GLMM in table 3.1 with binomial error structure and individual identity as a random term ( $n = 362$  males; variance = 1.28). Estimates for continuous fixed terms were calculated from standardized input variables. <sup>a</sup> = age-corrected; <sup>b</sup> = week-corrected and across the population.

### 3.4.2 Duration of prospecting forays

Subordinate males typically returned to their own groups on the same day they departed on prospecting forays (73% of forays). Prospectors were more likely to return to their group on the same day as their departure when their group was babysitting and when they had encountered another group (figure 3.3; table 3.4). Including a prospecting male's age and age-corrected body mass did not improve the fit of the best model (table 3.3) and total rainfall over the past month produced models with relatively high AIC values ( $\Delta_i > 25$ ; table 3.3), which suggested that these predictors had no influence on whether or not prospectors returned on the same day as they departed.



**Figure 3.3:** Effects of whether or not a prospector's group was (a) babysitting and (b) involved in an intergroup interaction on the probability that prospector's returned to their own groups on the same day as they departed on a foray. Predictions were estimated from the GLMM in table 3.4, setting the predictor not graphed to zero. Error bars are prediction intervals (SE) accounting for the uncertainty in the estimates of the fixed effects.

Fixed terms	$\log(L)$	d.f.	AIC	$\Delta_i$
I + B	-1301.70	4	2611.39	0.00
A + M + I + B	-1301.61	6	2615.22	3.83
B	-1310.30	3	2626.59	15.20
A + M + B	-1309.86	5	2629.71	18.32
I + R	-1314.50	4	2637.00	25.61
I	-1316.23	3	2638.46	27.07
A + M + I	-1316.05	5	2642.10	30.71
R	-1321.89	3	2649.77	38.38
A + M + R	-1321.32	5	2652.64	41.25
A + M	-1323.19	4	2654.38	42.99

**Table 3.3:** Candidate models for the factors influencing the duration of prospecting forays by subordinate males. For all models: A = age; M = age-corrected body mass; I = intergroup interaction; B = babysitting; R = total rainfall in previous month. All GLMMs were fitted with whether or not a male returned to his group on the same day that he departed on a prospecting foray ( $n = 2304$  forays) as the binary response variable and included individual identity ( $n = 271$  males) as a random term.

Fixed terms	Estimate $\pm$ SE	$z$	$P$
(Intercept)	$0.76 \pm 0.08$	9.90	
Intergroup interaction (yes)	$0.50 \pm 0.12$	4.09	< 0.001
Babysitting (yes)	$0.61 \pm 0.12$	5.29	< 0.001

**Table 3.4:** Factors affecting the duration of prospecting forays by subordinate males. Results from the best GLMM in table 3.3 with binomial error structure and individual identity as a random term ( $n = 271$  males; variance = 0.30).

### 3.5 Discussion

The timing of extraterritorial prospecting forays by subordinate male meerkats broadly followed a seasonal pattern, which was correlated with, but not predicted exclusively by, periods of low accumulated rainfall, high female fertility and subordinate female evictions. Moreover, the timing of forays did not appear to be influenced by cues from within a male's own group on the potential availability of extra-group mating and dispersal opportunities. In addition to the broad seasonal pattern, a male's probability of prospecting was positively correlated with his age, age-corrected body mass, and periods when encounters with neighbouring groups occurred. The distance between groups also affected the duration of forays, as males were more likely to return on the same day as they departed when their group was involved in an intergroup interaction. Prospectors were also more likely to return on the same day as they departed when their group was babysitting, which was associated with an increased likelihood of relocating their own group. Together, my results suggest that patterns of prospecting by subordinate males are highly seasonal and cannot be predicted by simple measures of recent rainfall, patterns of fertility or potential dispersal opportunities; yet investment in prospecting does appear to be influenced by the proximity between groups, the availability of dispersal opportunities and the costs associated with extraterritorial prospecting.

Population- and group-level measures of dominant female oestrus and subordinate female evictions were relatively poor predictors of the timing of prospecting events, in contrast to a simple function of week. As the dominant female's oestrus is typically short in meerkats (approximately four days) and does not overlap the period when she is actively evicting her subordinate females (i.e., the latter stages of pregnancy; Clutton-Brock et al. 1998a; Kutsukake and Clutton-Brock



2006b), it may be unfeasible for males to attempt to time their prospecting forays to specific oestrus or eviction periods. Similarly, if oestrus and eviction patterns are not synchronized among groups, cues from within each group are unlikely to be reliable indicators of population trends. Males may, therefore, have evolved a strategy that involves spreading their investment in prospecting over the whole breeding season, with timing responding to a highly predictable seasonal cue such as photoperiod, as suggested for dispersal in other species (Dufty and Belthoff 2001). This strategy may ultimately increase the likelihood of encountering both mating and dispersal opportunities in species where a typical breeding season spans several months, females give birth to multiple litters per breeding season, and subordinate females are evicted over extended periods of time, as occurs in meerkats (Clutton-Brock et al. 1999b). Nevertheless, the positive effect of the number of evicted females across the population (adjusted for week) on the probability of prospecting suggests that subordinate males may also be responding to a perception of dispersal opportunities, as these depend in large part on encounters with evicted females (Clutton-Brock et al. 2008).

In addition to the consistent seasonal pattern of prospecting and the effect of subordinate female evictions, subordinate males were more likely to prospect on weeks when their groups encountered another group. Although fortuitous encounters between groups presumably allow subordinate individuals to assess dispersal opportunities and copulate with extra-group individuals in many species (e.g., common marmosets: Lazaro-Perea 2001; ursine colobus monkeys: Teichroeb et al. 2011), males may also actively lead their groups into these encounters (e.g., banded mongooses: Cant et al. 2002). Indeed, subordinate male meerkats have been observed leading their groups in the direction of a neighbouring group's territory prior to an intergroup interaction, in addition to prospecting immediately after an intergroup interaction (personal observation). The correlation between intergroup interactions and the probability of prospecting, therefore, suggests that the general proximity between neighbouring groups is important in the timing of prospecting forays, in addition to the evident importance of the interactions *per se*. The distance between suitable habitat patches (or between groups in group-living species) is expected to affect the costs associated with dispersal movements (Hanski et al. 2000) and may influence dispersal rates (Bowler and Benton 2009). My results suggest that

intergroup (i.e., inter-patch) distance is likely to be important in the timing of prospecting forays as well, presumably because prospecting when neighbouring groups are nearby reduces the search time typically associated with extraterritorial movements, thereby lowering the cost of prospecting.

An important role of the costs of extraterritorial forays in determining a male's investment in prospecting is also supported by my finding that heavier males were more likely to prospect than lighter males. A positive correlation between body mass and dispersal has also been described in many species (e.g., Belding's ground squirrels: Nunes et al. 1999; greater flamingos: Barbraud et al. 2003), as dispersers presumably require high energy reserves to cope with the costs typically associated with dispersal (reviewed in Dufty and Belthoff 2001). Similarly, heavier individuals may be able to invest more in prospecting if they are better able to cope with the energetic costs of extraterritorial movements (e.g., Young et al. 2005) and with the costs associated to aggressive encounters with extra-group individuals (e.g., Raihani et al. 2010), common to both prospecting and dispersal processes.

The costs of extraterritorial forays are likely to increase with the amount of time prospectors spend away from their groups, as individuals are more vulnerable to predation and less likely to be able to forage efficiently when alone (e.g., Ridley et al. 2008). Males, therefore, should attempt to minimize the amount of time they spend away from their groups during prospecting forays. Accordingly, I found that prospectors typically returned to their groups on the same day that they departed on a foray, and did so more frequently when their groups were babysitting and when their groups were involved in an intergroup interaction on the day of departure. As groups that are babysitting consistently use the same overnight burrow over several weeks (Clutton-Brock et al. 2000; Turbé 2006), prospectors may be able to find their own groups more easily upon returning from a foray when their groups are babysitting. This idea is supported by observations of prospectors following straight paths directly to the overnight burrow last used by their group when returning from a foray (personal observation). Prospecting when neighbouring groups are close may also increase the probability that prospectors will find their own groups upon returning from a foray, by reducing the distance prospectors have to travel away from, and potentially back to, their own group.

Although they conducted more prospecting forays in general, heavier and older males were equally likely to return to their group on the same day as they departed as their lighter and younger counterparts. This suggests that improved condition (body mass) and a greater knowledge of their own and surrounding territories (age) did not necessarily confer an advantage in terms of longer forays being conducted. As meerkats benefit from the warmth of other group members during the night (Müller and Lojewski 1986), spending the night alone is likely to pose an additional, high energetic cost for prospecting males, particularly during the colder months of a prospecting season (May to September). The duration of prospecting forays may, therefore, be constrained by the high energetic costs of extraterritorial movements (e.g., reduced thermoregulatory and foraging capabilities) and depend primarily on the ease with which prospectors are able to locate neighbouring groups and their own groups upon returning from forays.

Taken together, my results suggest that the timing of and investment in prospecting by subordinate males is largely influenced by the benefits and costs of extraterritorial movements. Investigating the factors that modulate investment in prospecting by subordinate individuals is likely to increase our understanding of the patterns of subordinate reproduction, dispersal and contributions to helping observed in cooperative breeders (e.g., Double and Cockburn 2003; Young et al. 2005; Young et al. 2007; Clutton-Brock et al. 2008). To my knowledge, this is the first study to investigate the individual variation in prospecting by subordinate individuals using a comprehensive range of ecological, social and individual factors.



## CHAPTER 4

# Alternative developmental trajectories in males: to prospect or to help?

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### 4.1 Abstract

In cooperatively breeding societies, subordinate individuals are often faced with the trade-off between investing in helping to rear offspring that are not their own and attempting to breed themselves. The magnitude of this trade-off is likely to be determined by the relative payoffs from the two behaviours (i.e. helping and mating), which could be influenced by conditions experienced early in life: an individual born in good condition, for example, may invest more in mating rather than helping. Whether differences in early-life conditions result in individual differences in propensity to help or prospect later in life, however, is as yet unknown. In this study, I investigate the effects of early-life body mass of male meerkats on the age of onset of

extraterritorial prospecting and on subsequent contributions to two key helping behaviours, pup feeding and raised guarding. I show that males that are heavier early in life begin prospecting at an earlier age and contribute less to feeding pups later in life than lighter males. These reduced contributions to pup feeding by heavier males do not appear to arise from direct energetic trade-offs between prospecting and helping or from differences in body mass later in life. My results suggest that, in meerkats, males may follow alternative developmental trajectories, which appear to be condition-dependent and to modulate investment in prospecting and helping behaviours.

## **4.2 Introduction**

Individuals are typically confronted with the choice of allocating a finite amount of energy and time to different activities, with decisions often leading to trade-offs between behaviours (Cuthill and Houston 1997). The trade-off between investing in parental care and mating, for example, is likely to occur when males have access to multiple breeding opportunities (Westneat et al. 1990; Webster 1991; Magrath and Komdeur 2003). In cooperatively breeding societies, similar trade-offs may occur between helping to rear the offspring of others and attempting to breed independently (Emlen 1982). As cooperative activities and mating-related activities (e.g., provisioning food to young and prospecting for mates, respectively) are costly (reviewed in Heinsohn and Legge 1999; e.g., Young et al. 2005) and investment in either may be size-dependent (e.g., Clutton-Brock et al. 2002; Chapter 3), males are unlikely to be able to invest significantly in both at any given time. Indeed, recent studies on cooperative breeders suggest that subordinate males trade off their current investment in helping and prospecting (Young et al. 2005; Young et al. 2007; Williams and Hale 2007). Although decisions regarding whether to invest in prospecting over helping behaviours may depend largely upon the current availability of mating or dispersal opportunities (Chapter 3), individual differences in propensity to invest in one or the other may also play an important role (Komdeur 2006; Bergmüller et al. 2010).

Individuals are likely to differ in their investment in breeding (e.g., prospecting) and helping behaviours in accordance with the relative payoffs from the

two behaviours (Cant and Field 2001). In addition to current condition (Heinsohn and Legge 1999), these relative payoffs could be influenced by conditions experienced early in life, which are expected to have long-term fitness consequences (Lindström 1999). For example, individuals that are heavier in early life develop greater foraging efficiency, which is maintained in later life (Ridley 2007; Thornton 2008), and may be more likely than lighter individuals to acquire dominance and reproduce as adults (Russell et al. 2007; Hodge et al. 2008). Similarly, body mass in early life may also affect the timing of natal dispersal (e.g., Nunes et al. 1999; Barbraud et al. 2003). Given the importance of early-life body mass in this range of contexts later in life, it might also be expected to have downstream effects on subordinate individuals' investment in prospecting and helping behaviours. Evidence for an effect of early-life conditions on future contributions to helping behaviours has been recently found in meerkats, where females that receive more care as pups invest less in helping later in life than those that receive less care (English 2009). Females that receive more care as pups may be more likely to breed as adults, and thus invest less in costly helping behaviours throughout their lives to maintain good body condition. The extent to which differences in early-life body mass can lead to alternative developmental trajectories among males, who face the trade-off between prospecting and helping, remains largely unexplored.

In this study, I examine whether conditions in early life can modulate the investment in breeding and helping behaviours later in life in cooperative breeders. Specifically, I investigate the effects of early-life body mass on the age of onset of extraterritorial prospecting behaviour and on later investment in two key helping behaviours, pup feeding and raised guarding, in male meerkats. Both pup feeding and raised guarding are expected to contribute to offspring survival (Clutton-Brock et al. 2001c) and may lead to indirect fitness benefits (Hamilton 1964) and direct benefits through group augmentation (Kokko et al. 2001). Raised guarding may provide the additional benefit of enhancing an individual's own survival (Bednekoff 1997; Clutton-Brock et al. 1999c) and meerkats are frequently vigilant regardless of whether or not there are pups in the group. By investing in extraterritorial prospecting during the breeding season, subordinate males may gain direct fitness benefits through copulations with extra-group females, and can gather information on future dispersal opportunities (Young et al. 2007; Chapter 3). Males begin prospecting and

contributing to helping after achieving nutritional independence at approximately three months of age (Brotherton et al. 2001), but levels of investment in both behaviours remain relatively low until approximately one year of age (Clutton-Brock et al. 2002). Previous work suggests that males and females that are heavier at nutritional independence disperse and attempt to breed earlier in life than lighter individuals (Russell et al. 2007). However, it is unknown whether early-life differences in body mass among males lead to divergent levels of investment in prospecting and helping behaviours later in life. Here, I first investigate whether early-life body mass affects an individual's subsequent investment in prospecting and helping behaviours and assess the evidence for alternative developmental trajectories with individuals specialising more in one behaviour than the other according to their early-life body mass. I conclude by examining whether the effects of early-life body mass on prospecting and helping later in life can simply be attributed to the correlation between early-life body mass and a male's body mass at the time of helping or prospecting.

## **4.3 Methods**

### **4.3.1 General data collection**

Groups were visited at least once every three days from 1998 to 2009 as part of a long-term study and life history events such as birth, emigration and immigration were typically known to the day. Encounters with neighbouring groups (intergroup interactions) and the presence or absence of group members were noted on each visit, which lasted 2 – 4 h in the morning (after groups started foraging) and 1 – 2 h in the evening (before groups returned to their overnight burrow). Subordinate males that were temporarily absent from their group, with no prior signs of illness or aggression from their group, were considered to be prospecting.

During visits to groups, most individuals were weighed in the morning before the group started foraging. Individuals were trained to step on an electronic balance for small rewards of water or crumbs of hard boiled egg, which allowed the recording of body mass to an accuracy of 1 g. I used the average of all mass measurements



taken for a male between 90 and 120 days of age (approximate onset of nutritional independence; Brotherton et al. 2001), as his measure of early-life body mass.

#### **4.3.2 General statistical methods**

All statistical analyses were conducted using R (version 2.13; R Development Core Team 2011) with *coxme* (version 2.1-3; Therneau 2011) for building mixed-effects Cox regression models and *lme4* (version 0.999375-40; Bates et al. 2011) and *glmmADMB* (version 0.6.4; Skaug et al. 2011) for generalized linear mixed models (GLMM). Model selection and comparison (see details below) were achieved using Akaike's information criterion values (AIC; Akaike 1973), corrected for small sample sizes (AICc; Burnham and Anderson 2002). I calculated the AICc differences ( $\Delta_i$ , the model's AICc minus the minimum AICc among candidate models) for each model and considered those with  $\Delta_i$  less than two to be the 'best', opting for simpler models (those with fewer estimated parameters) when more than one model had  $\Delta_i < 2$  and similar fits to the data (log-likelihood; Burnham and Anderson 2002). I standardized continuous input variables by subtracting the mean and dividing by two standard deviations (SD), to allow the comparison of their estimated effect sizes with those of binary predictors and facilitate the interpretability of interactions (Gelman and Hill 2007; Schielzeth 2010).

#### **4.3.3 Early-life body mass and investment in prospecting**

To determine the effect of early-life body mass on the age at which males start prospecting, I obtained the first recorded prospecting foray for a total of 468 males. Males included in the study were born between 1997 and 2008, survived beyond nutritional independence (121 days of age), and subsequently within 18 months after birth either (a) prospected: temporarily left their natal group on an extraterritorial foray ( $n = 261$  males), emigrated in a coalition of males ( $n = 13$  males) or were last seen approaching another group ( $n = 2$  males); or (b) did not prospect: died ( $n = 91$  males) or were no longer observed ( $n = 101$  males), which includes males that survived beyond 18 months of age, survived to the end of the study or whose groups were no longer studied, having not yet prospecting or emigrated. Death was confirmed for 26% of the individuals that died before prospecting in (b), and assumed for the remainder, given that they disappeared from their groups alone and outside of the

breeding season (Russell et al. 2007; Young et al. 2007). I considered events occurring up to 18 months of age, as this represents the age at which approximately 50% of subordinate males have prospected.

Given the complex nature of the data, where the likelihood of prospecting increases with age (Chapter 3), but males may exit the study before prospecting (either through death or because they were no longer observed), I investigated the effect of body mass at nutritional independence ( $\bar{x}$  = 339 g, SD = 47.6) on the age of onset of prospecting using Cox regression models (O'Quigley 2008). In order to incorporate into the models predictors which vary over time (time-dependent) and may influence the probability of prospecting (e.g., season; Young et al. 2007), I divided the data for each male into weeks, starting at nutritional independence up to the occurrence of the event (a) or until they were censored (b) (see above). Each week, therefore, could include weekly measures of group size ( $\bar{x}$  = 19 individuals > 90 days old, SD = 7.4), whether or not the individual's group had an intergroup interaction, and total rainfall over the past month ( $\bar{x}$  = 23 mm, SD = 28.3). Month of the year (with years beginning in April and ending the following March; see Chapter 3) was also included in the models as a continuous predictor with a quadratic term, due to its expected non-linear effect on the probability of prospecting (Young et al. 2007; Chapter 3). All candidate models (table 4.1) included mother and litter identities as random terms to account for repeated measures.

To substantiate whether the age of onset of prospecting behaviour is an indication of rates of prospecting in early life, I tested whether the age at which a male first prospected was correlated with the number of prospecting events recorded up to 18 months of age (divided by the number of days observed) by conducting a Pearson's correlation test. For this analysis, I used a subset of 196 subordinate males that prospected at least once before 18 months of age, all of whom survived and were monitored continuously until 18 months of age.

#### **4.3.4 Early-life body mass and investment in helping**

To determine whether early-life body mass is correlated with early-life investment in raised guarding and pup feeding, I conducted focal observations on 50 subadult males (range 208 – 370 days old) in 12 different groups from September 2008 – January 2009 and August – November 2009. I conducted between four and six 30 min focal

observations per individual, each on a different day, while groups were foraging without pups or with pups that were within the peak pup feeding period (40 – 65 days old). Focal observations were only conducted when over 50% of the group was actively foraging. To exclude the potential negative effects of current prospecting effort on cooperative activities (Young et al. 2005), observations were conducted no less than six days after a prospecting event if a focal male had prospected. Behaviours were recorded on a handheld computer (Organiser II LZ64; Psion Teklogix, UK), with times accurate to 1 s. For all focal individuals, I recorded the duration of all occurrences of raised guarding (i.e., vigilant from a raised position; Clutton-Brock et al. 1999c). Additionally, for a subset of 30 males in 11 groups with foraging pups, I recorded all successful foraging attempts by the focal individual, as well as the size of the prey found and whether or not it was fed to a pup. Prey were classified into five broad size categories (size and mean wet mass: tiny = 0.05 g, small = 0.11 g, medium = 0.58 g, large = 2.86 g and extra large = 9.56 g; Thornton 2008), which were then used to determine the total biomass fed to pups. Occasions when several prey were found clustered together were treated as a single foraging attempt and the combined prey were considered as a single food item.

*Effect of early-life body mass on pup feeding.* I measured the effect of a male's body mass at nutritional independence on the proportion of food items found that he subsequently fed to a pup (termed 'generosity'), and the rate at which he fed pups (g/h). A first set of GLMMs with binomial error structure and logit link function was used to investigate the factors affecting a male's generosity, by fitting the total number of food items fed to pups (numerator) and the total number of food items found per observation session (denominator) as the proportional response variable. Individual and group identities were fitted as the random terms in all candidate models (table 4.3a), that included different combinations of the following input variables: the focal male's body mass at nutritional independence ( $\bar{x}$  = 371 g, SD = 31.6), age on observation date ( $\bar{x}$  = 285 days old, SD = 32.2), the group size ( $\bar{x}$  = 10 individuals > 90 days old, SD = 2.4), the number of pups in the group ( $\bar{x}$  = 4 pups, SD = 1) and the total rainfall in the past month ( $\bar{x}$  = 18 mm, SD = 16.9). A second set of GLMMs with negative binomial error structure was used to investigate the factors affecting a male's pup feeding rate, by fitting the total biomass (g) fed to pups as the response variable, accounting for the duration of each observation session (30 min) as

an offset in the models. All candidate models (table 4.3b) included the random terms and similar combinations of the input variables as the models for male generosity. To control for the potentially confounding effect of current prospecting effort on pup feeding, models for both analyses also included whether or not the focal male had prospected within 30 days before the focal observation, as a predictor.

*Effect of early-life body mass on raised guarding.* I measured the effect of body mass at nutritional independence on the proportion of observation time males spent on raised guard. Number of minutes spent on raised guard (numerator) and the total minutes observed per session (denominator) were fitted as the proportional response variable in binomial GLMMs with logit link function. Individual and group identities were fitted as the random terms in all candidate models (table 4.5), that included different combinations of the following input variables: the focal male's body mass at nutritional independence ( $\bar{x}$  = 366 g, SD = 31.4), age on observation date ( $\bar{x}$  = 308 days old, SD = 38.1), the group size ( $\bar{x}$  = 13 individuals > 90 days old, SD = 4.6) and the total rainfall in the past month ( $\bar{x}$  = 13 mm, SD = 15.4). To control for the potentially confounding effect of current prospecting effort on raised guarding, the models also included whether or not the focal male had prospected within 30 days before the focal observation, as a predictor. All models were fitted with two-way interactions between whether or not there were pups foraging with the group on the day of the focal observation and all other predictors included in each model.

#### **4.3.5 The mechanism of early-life body mass effects on prospecting and helping**

The simplest explanation for the effects of early-life body mass on prospecting and helping behaviours is that males that are heavier at nutritional independence are consistently heavier than lighter males throughout their lives (Russell et al. 2007) and as such, are able to invest more in costly prospecting and cooperative behaviours. To test this idea, I first estimated the correlation between body mass at nutritional independence (3 months of age) and body mass at 6 and 12 months of age (i.e., the period within which both prospecting and helping behaviours were measured). I then examined whether replacing a male's body mass at nutritional independence with his age-corrected body mass at the time that the behaviour in question (i.e., prospect or not, pup feeding and raised guarding) was measured, improved the fit of the original best models to the data.

To obtain a male's age-corrected body mass, I first calculated a predicted body mass at each age for each male included in the original analyses (see above). I used predicted measures instead of actual mass records, as body mass records obtained in the field were not available for every day and using them would have significantly reduced my sample sizes for the analyses. Predicted body mass was obtained from a biphasic growth model (English et al. 2011), using morning body mass records from 1064 males and females ( $n = 280260$  records of body mass), excluding measurements from females in the latter stages of pregnancy ( $< 40$  days to parturition or abortion; S. Sharp and T. Clutton-Brock, unpublished manuscript). I then subtracted the mean predicted body mass across all individuals for a given age to obtain age-corrected body mass.

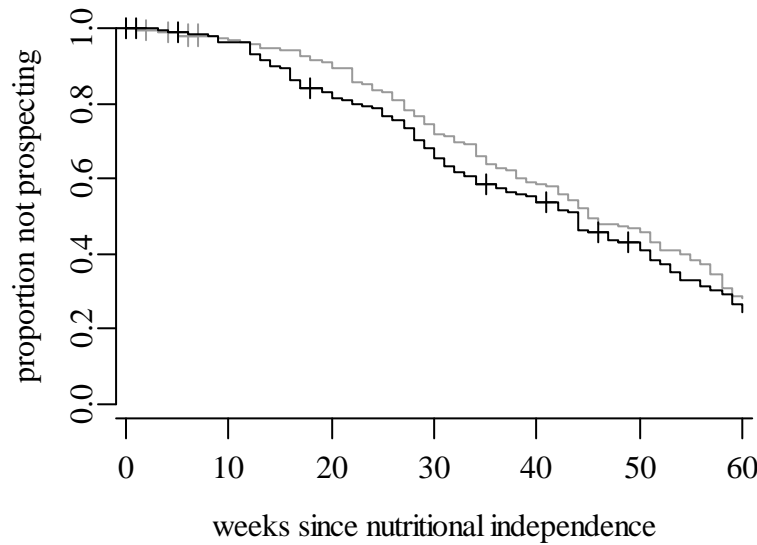
Owing to insufficient body mass records for obtaining a growth curve for some of the males included in the original analyses, I was not able to estimate age-corrected body mass for all of them. I therefore, refit the best models from the analyses above (using body mass at nutritional independence) with the reduced data sets (see below), to be able to compare their fit with models that incorporated age-corrected body mass. For the mixed-effects models of contributions to helping ( $n = 27$  and 47 males in 11 and 12 groups for pup feeding and raised guarding, respectively), age-corrected body mass was included as a single measure on the day of the focal observation (see above). For the Cox regression model of the age of onset of prospecting ( $n = 432$  males from 254 litters and 88 mothers), age-corrected body mass was fitted as a time-dependent predictor in each week of observation (see above).

## **4.4 Results**

### **4.4.1 Early-life body mass and investment in prospecting**

Males that were heavier early in life began prospecting at an earlier age than lighter males (figure 4.1). When controlling for the effects of month and occurrence of an intergroup interaction in the best mixed-effects Cox regression model (table 4.1), body mass at nutritional independence had a strong positive effect on the probability of prospecting at a given age later in life (table 4.2). As expected, males that were younger when conducting their first prospecting foray, conducted forays at higher

rates within the first 18 months of life (Pearson's correlation test:  $t = -3.72$ , d.f. = 194,  $P < 0.001$ ;  $n = 196$  males).



**Figure 4.1:** Proportion of heavy ( $> \bar{x}$  body mass; black,  $n = 233$  individuals) and light ( $\leq \bar{x}$  body mass; grey,  $n = 235$  individuals) subordinate males, as weighed at nutritional independence, that had not prospected by each week since independence (approximately 17 weeks of age). Curves were estimated using the Kaplan-Meier survivorship function. Crosses indicate censored data (males that died, were no longer observed or reached 18 months of age, having not yet prospected).

Fixed terms	$\log(L)$	d.f.	AICc	$\Delta_i$
EBM + IGI + MO + MO <sup>2</sup>	-1390.97	6	2793.95	0.00
EBM + IGI + R + MO + MO <sup>2</sup>	-1390.03	7	2794.07	0.12
EBM + IGI + GS + MO + MO <sup>2</sup>	-1390.22	7	2794.45	0.50
EBM + IGI + GS + R + MO + MO <sup>2</sup>	-1389.41	8	2794.84	0.88
IGI + MO + MO <sup>2</sup>	-1396.46	5	2802.91	8.96
IGI + R + MO + MO <sup>2</sup>	-1395.64	6	2803.28	9.32
IGI + GS + MO + MO <sup>2</sup>	-1395.91	6	2803.83	9.87
IGI + GS + R + MO + MO <sup>2</sup>	-1395.20	7	2804.41	10.45

**Table 4.1:** Candidate models for the factors affecting the age of onset of prospecting behaviour. All Cox regression models were fitted with whether or not a male prospected on a given week ( $n = 468$  males) as the response variable and included mother ( $n = 92$  mothers) and litter ( $n = 262$  litters) identities as random terms. For all models: EBM = early-life body mass; GS = group size; IGI = intergroup interaction; MO = month; R = total rainfall in past month.

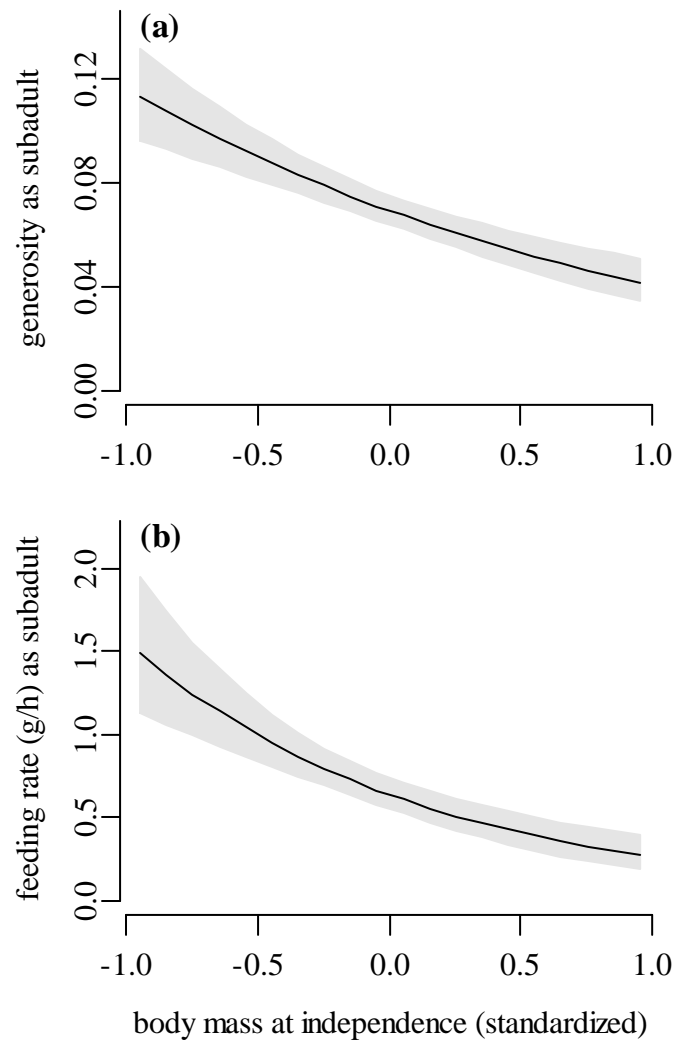
Fixed terms	Estimate $\pm$ SE	$\exp(\text{Est.})$	$z$	$P$
Early-life body mass	$0.54 \pm 0.16$	1.70	3.31	$< 0.001$
Intergroup interaction (yes)	$1.49 \pm 0.14$	4.44	10.99	$< 0.001$
Month <sup>2</sup>	$-2.05 \pm 0.37$	0.13	-5.55	$< 0.001$
Month	$-0.08 \pm 0.16$	0.92	-0.52	

**Table 4.2:** Factors affecting the age of onset of prospecting in subordinate males. Results from the best mixed-effects Cox regression model ( $n = 468$  males) in table 4.1 with mother ( $n = 92$  mothers; variance = 0.70) and litter ( $n = 262$  litters; variance = 0.27) identities as random terms. Estimates for continuous fixed terms were calculated from standardized input variables.

#### 4.4.2 Early-life body mass and investment in helping

*Effect of early-life body mass on pup feeding.* Males that were heavier early in life were less generous and fed pups at lower rates later in life, than lighter males (figure 4.2). When controlling for the effects of the number of pups in the group and total rainfall in the past month (for generosity only) in the best GLMMs (table 4.3), a male's body mass at nutritional independence had strong negative effects on both the proportion of food items he fed to pups (generosity) and his pup feeding rate (g/h) as a subadult (6 – 12 months of age; table 4.4). Models which included whether males had prospected within the 30 days leading up to the focal observation (table 4.3) did not produce better fits than the models in table 4.4, indicating that there was no difference in generosity or pup feeding rates between males that had prospected recently and those that had not.

*Effect of early-life body mass on raised guarding.* Body mass at nutritional independence had no effect on the proportion of time males spent on raised guard as subadults (GLMM number 5 in table 4.5: effect of early-life body mass  $\pm$  standard error (SE) =  $-0.05 \pm 1.70$ ,  $z = -0.03$ ; interaction with the presence of pups =  $-0.43 \pm 2.02$ ,  $z = -0.21$ ,  $P = 0.830$ ), when controlling for the effect of the interaction between group size and the presence of pups foraging with the group (effect  $\pm$  SE =  $5.89 \pm 1.90$ ,  $z = 3.09$ ,  $P = 0.002$ ). Including whether males had prospected within the 30 days leading up to the focal observation did not improve the fit of the best model in table 4.5, indicating that there was no difference in time spent on raised guard between males that had prospected recently and those that had not.



**Figure 4.2:** Effects of early-life body mass on (a) generosity (proportion of food items found that were fed to pups) and on (b) pup feeding rates (g/h) among subadult males. Predictions were estimated from the GLMMs in table 4.4, using means of predictors not graphed. Shaded areas are prediction intervals (SE) accounting for the uncertainty in the estimates of the fixed effects. Body mass was standardized by subtracting the mean and dividing by two standard deviations.



Response term	Fixed terms	log(L)	d.f.	AICc	$\Delta_i$
(a) Generosity	EBM + nP + R	-116.75	6	245.99	0.00
	EBM + nP + GS + R	-116.29	7	247.24	1.25
	EBM + F + nP + R	-116.73	7	248.13	2.14
	EBM + F + nP + GS + R	-116.25	8	249.36	3.37
	EBM + A + nP + GS + R	-116.27	8	249.41	3.42
	nP + GS + R	-118.91	6	250.32	4.33
	EBM + F + A + nP + GS + R	-116.22	9	251.52	5.53
	A + nP + GS + R	-118.89	7	252.44	6.45
	nP + R	-121.57	5	253.49	7.50
(b) Feeding rate	EBM + nP	-132.11	6	276.72	0.35
	EBM + F + nP	-130.85	7	276.37	0.00
	EBM + F + nP + GS	-130.60	8	278.05	1.68
	EBM + nP + GS	-131.87	7	278.41	2.04
	EBM + F + nP + GS + R	-130.09	9	279.25	2.88
	EBM + nP + GS + R	-131.23	8	279.31	2.94
	EBM + F + A + nP + GS + R	-129.90	10	281.13	4.75
	nP + GS	-134.33	6	281.15	4.78
	EBM + A + nP + GS + R	-131.22	9	281.52	5.15
	nP + GS + R	-133.56	7	281.79	5.42
	nP	-136.53	5	283.41	7.04
	A + nP + GS + R	-133.55	8	283.95	7.58

**Table 4.3:** Candidate models for the factors affecting male contributions to pup feeding. GLMMs were fitted with binomial (a) and negative binomial (b) error structures and all models included group ( $n = 11$  groups) and individual ( $n = 30$  males) identities as random terms. For all models ( $n = 177$  observations): A = age; EBM = early-life body mass; GS = group size; nP = number of pups; R = total rainfall in past month; F = recent prospecting foray.

Response term	Fixed terms	Estimate $\pm$ SE	$z$	$P$
(a) Generosity	(Intercept)	-2.60 $\pm$ 0.09	-29.89	
	Early-life body mass	-0.56 $\pm$ 0.18	-3.14	0.002
	Number of pups	0.39 $\pm$ 0.14	2.78	0.005
	Rainfall in past month	0.39 $\pm$ 0.15	2.56	0.010
(b) Feeding rate	(Intercept)	-8.64 $\pm$ 0.15	-58.81	
	Early-life body mass	-0.89 $\pm$ 0.30	-2.98	0.003
	Number of pups	1.09 $\pm$ 0.25	4.40	< 0.001

**Table 4.4:** Factors affecting subadult male contributions to feeding pups. Results from the best GLMMs in table 4.3 with binomial (a) and negative binomial (b) error structures, and with group ( $n = 11$  groups; variance = 0.00) and individual ( $n = 30$  males; variance = 0.00) identities as random terms in both models ( $n = 177$  observations). Estimates for continuous fixed terms were calculated from standardized input variables.

Fixed terms	$\log(L)$	d.f.	AICc	$\Delta_i$
GS * P	-384.71	6	781.71	0.00
(GS + R) * P	-382.62	8	781.75	0.04
(A + GS + R) * P	-381.06	10	782.90	1.19
(EBM + GS + R) * P	-382.47	10	785.71	4.00
(EBM + GS) * P	-384.62	8	785.74	4.03
(EBM + A + GS + R) * P	-380.69	12	786.50	4.79
(EBM + F + GS + R) * P	-381.88	12	788.88	7.17
(EBM + F + GS) * P	-384.22	10	789.22	7.51
(EBM + F + A + GS + R) * P	-380.06	14	789.62	7.91

**Table 4.5:** Candidate models for the factors affecting male contributions to raised guarding. All GLMMs were fitted with a binomial error structure and all models included group ( $n = 12$  groups) and individual ( $n = 50$  individuals) identities as random terms. For all models ( $n = 294$  observations): A = age; EBM = early-life body mass; GS = group size; P = pups or no pups; R = total rainfall in past month; F = recent prospecting foray.

#### 4.4.3 The mechanism of early-life body mass effects on prospecting and helping

Males that were heavy at nutritional independence (3 months of age) maintained their body mass advantage over light males at 6 months (Pearson's correlation test:  $t = 27.92$ , d.f. = 415,  $P < 0.001$ ;  $n = 417$  males) and 12 months of age (Pearson's correlation test:  $t = 15.43$ , d.f. = 369,  $P < 0.001$ ;  $n = 371$  males).

Refitting the best model of factors affecting the age of onset of prospecting (table 4.1), but incorporating a male's age-corrected body mass at each week of observation rather than his body mass at nutritional independence, produced a better model (i.e., lower AICc; table 4.6). This result indicates that a male's current age-corrected body mass accounts for considerably more variation in the age of onset of prospecting than his early-life body mass. In contrast, the best models of factors affecting generosity and feeding rates (table 4.3) fitted with body mass at nutritional independence explained more variation than models fitted with age-corrected body mass at the time the behaviours were measured (6 – 12 months of age; table 4.6). Incorporating a male's age-corrected body mass to the best model of factors affecting his contribution to raised guarding (table 4.5) did not improve the fit of the model (table 4.6).

Response term	Fixed terms	log(L)	d.f.	AICc	$\Delta_i$
<i>Investment in prospecting</i>					
(a) Age of onset	ACBM + IGI + MO + MO <sup>2</sup>	-1286.60	6	2585.20	0.00
of prospecting	EBM + IGI + MO + MO <sup>2</sup>	-1297.40	6	2606.80	21.59
<i>Contributions to helping</i>					
(b) Generosity	EBM + nP + R	-105.35	6	223.25	0.00
	ACBM + nP + R	-109.48	6	231.51	8.26
(c) Feeding rate	EBM + nP	-126.80	6	266.16	0.00
	ACBM + nP	-128.09	6	268.73	2.57
(d) Time on raised guard	GS * P	-295.83	6	603.98	0.00
	(ACBM + GS) * P	-294.89	8	606.31	2.34

**Table 4.6:** Model comparisons between original best models in tables 4.1, 4.3 and 4.5, and models with age-corrected body mass at the time behaviours were measured fitted as a fixed term. Paired models were fitted to the same datasets. Models in (a) include mother and litter identities, and models in (b), (c) and (d) include individual and group identities as random terms. For all models: ACBM = age-corrected body mass; EBM = early-life body mass; GS = group size; IGI = intergroup interaction; MO = month; nP = number of pups; P = pups or no pups; R = total rainfall in past month.

## 4.5 Discussion

My results suggest that in meerkats, young males may follow alternative developmental trajectories that appear to be condition-dependent. I found that the age of onset of prospecting is positively correlated with body mass at nutritional independence (three months old), while contributions to pup feeding as subadults (6 to 12 months old) are negatively correlated with the same measure of early-life body mass. In contrast, the amount of time males invest in raised guarding as subadults is not affected by early-life body mass. The reduction in helping effort among subadult males that were heavy in early life does not appear to be a simple by-product of an energetic trade-off between elevated prospecting effort and pup feeding. Similarly, although the correlation between body mass at nutritional independence and body mass later in life appears to explain the influence of early-life body mass on prospecting effort, this correlation does not seem to explain the effect of early-life body mass on contributions to pup feeding. I discuss the implications of my findings in light of the potential for the existence of alternative developmental trajectories in cooperative breeders, which in males may arise from the effects of early-life body mass on the expected relative payoff from investing in prospecting versus helping over a lifetime.

Male meerkats that were heavier at nutritional independence started prospecting earlier in life, and thus, conducted more extraterritorial forays than lighter males during their first 18 months of life. Conditions experienced early in life are expected to have long term fitness consequences in a wide range of species (Lindström 1999). However, few studies have investigated the downstream effects of early-life body mass on reproduction in cooperative breeders (e.g., Hodge 2005; Hodge et al. 2008) and only one such study focused on subordinate reproduction (Russell et al. 2007). Subordinate male meerkats seldom breed within their natal groups due to strong inbreeding avoidance, but are able to gain access to extra-group mating opportunities by conducting extraterritorial prospecting forays (O'Riain et al. 2000; Young et al. 2007; Spong et al. 2008). Evidence of a positive effect of body mass at nutritional independence on the age of onset of prospecting suggests a mechanism by which early-life body mass may impact positively on subordinate male reproductive success (Russell et al. 2007). By focusing solely on the effect of early-life body mass on the development of prospecting behaviour in males and excluding

the potentially confounding effects of early-life body mass on survival, the results presented here clarify previous findings by Russell et al. (2007).

In contrast to the positive effect of early-life body mass on investment in prospecting, males that were heavier at nutritional independence contributed less to pup feeding as subadults than males that were lighter, both in terms of feeding rate and proportion of food items found subsequently fed to pups (a measure of generosity). This result is perhaps surprising, as heavier individuals are typically found to contribute more given that helping is costly (Heinsohn and Legge 1999) and generally condition-dependent (Clutton-Brock et al. 2002). Such a negative correlation between early-life body mass and contributions to pup feeding might be explained if heavier males were simply investing more in prospecting, and therefore unable to invest in cooperative activities, due to the expected trade-offs in time and energy between these behaviours (Cuthill and Houston 1997; e.g., Young et al. 2005). However, analyses of the factors affecting a subadult male's contributions to helping controlled for whether the male had prospected during the preceding month, which had no effect, and, furthermore, data on contributions to helping were not collected within a week of a prospecting foray. These results, therefore, suggest a behavioural trade-off between prospecting and cooperative care in subordinate males that is independent of recent or current investment in prospecting and may be mediated by early-life differences in body mass.

A potential mechanism by which early-life body mass may exert downstream effects on investment in costly behaviours is through its effects on body mass later in life, if individual differences in body mass are maintained throughout life. Indeed, I found a strong positive correlation between a male's body mass at nutritional independence (three months of age) and his body mass at 6 and 12 months of age. Males that are heavier at nutritional independence, therefore, may subsequently invest more in prospecting because they are heavier throughout their first year of life and are potentially better able to cope with the energetic costs of prospecting (Young et al. 2005). The effect of early-life body mass on investment in prospecting through its effect on body mass later in life is supported by my finding that age-corrected body mass within the first 18 months of life explained more variation in the age of onset of prospecting than body mass at nutritional independence. Males that are heavy as subadults and thus, potentially more likely to breed independently, may be less likely

to invest in costly helping behaviours than light males in order to maintain their condition (Cant and Field 2001; Hodge 2007). Unlike investment in prospecting, however, individual differences in contributions to pup feeding between 6 and 12 months of age seem to be directly influenced by conditions experienced early in life: age-corrected body mass later in life is a poorer predictor of variation in generosity or feeding rates than body mass at nutritional independence.

Why investment in cooperative care by subordinate males would be determined by early-life conditions, rather than maintain flexibility, is currently unknown. One possibility is that potential differences in hormonal profiles between heavy and light individuals during early development may affect the expression of cooperative behaviours later in life (reviewed in Soares et al. 2010). Several studies have suggested that light males have lower androgen (e.g., testosterone) and higher glucocorticoids (e.g., cortisol) levels than heavy males (e.g., Duckworth et al. 2001; Liang and Zhang 2006; Pérez-Rodríguez et al. 2006). In adult male meerkats, plasma levels of cortisol are positively correlated with contributions to pup feeding (Carlson et al. 2006), while exposure to high levels of testosterone may lead to the suppression of parental behaviours (Wingfield et al. 1990). Males, therefore, could be ‘programmed’ during early development (Kapoor et al. 2006) to invest more or less in cooperative care later in life depending on their body mass and hormonal profiles in early life (Soares et al. 2010). In addition, given that high levels of cortisol are expected to compromise an individual’s immune response (e.g., Duckworth et al. 2001), prospecting may involve greater long-term costs for individuals that are light early in life than for those that are heavier. Ultimately, males in cooperatively breeding societies may be pursuing alternative life-history tactics that best suit their phenotypes (McNamara and Houston 1996; Stearns 1992) which may be determined early in life. In subordinate male meerkats, early-life differences in body mass may lead to distinct ‘stay and help’ and ‘stay and foray’ (Brown 1987) tactics later in life, in accordance with the relative payoffs from investing in either prospecting or helping.

Finally, in contrast to its effects on contributions to pup feeding and prospecting effort, a male’s body mass at nutritional independence had no effect on his contributions to raised guarding later in life. A male’s contribution to raised guarding as a subadult was also unaffected by his age-corrected body mass at the time

raised guarding effort was measured. For subordinate males, the benefits of pup feeding are likely to be primarily indirect (as males disperse from their natal groups) and the costs may be relatively high (Hodge 2007). Conversely, investment in raised guarding provides an immediate, direct benefit by lowering the risk of predation and is associated to relatively low costs (Bednekoff 1997; Clutton-Brock et al. 1999c). Daily variation in foraging success, therefore, may play a more important role in determining a male's contributions to raised guarding (Clutton-Brock et al. 1999c) than the measures of body mass used in my analyses. My results suggest that individual differences in contributions to different cooperative activities are likely to be influenced by the benefits and costs associated with each of the behaviours in question.

In conclusion, this study provides evidence of individual differences in levels of investment in breeding and cooperative behaviours among subordinate male meerkats, which appear to be explained in part by alternative, condition-dependent developmental trajectories. The growing interest in seeking to understand the causes of individual variation in contributions to cooperative activities and investment in breeding, therefore, may be well served by investigating the role of potentially formative effects of conditions experienced early in life.





## CHAPTER 5

# Individual contributions to territory defence: weighing up the benefits and costs

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*Note:* This chapter was prepared as a manuscript for submission to *Proceedings of the Royal Society B*. I designed the study and wrote the manuscript, while Andrew Young and Tim Clutton-Brock contributed to discussion.

### 5.1 Abstract

While investment in territory defence is expected to be influenced by its benefits, the additional role that costs may play is rarely considered. Here, we quantify both benefits and costs of repelling prospecting males in cooperative meerkats and demonstrate that both are required to explain the substantial variation in individual

contributions to defence observed. Males benefit more from repelling prospectors than females, as males may lose dominance and be expelled during intrusions. Accordingly, males invest the most in repelling prospectors. We also show that males experience an associated cost in the form of reduced weight gain and as such, heavier males contribute more to chasing prospectors. Finally, we show evidence of a cost not restricted to individuals engaged in chasing: both males and females reduce their contributions to pup feeding when prospectors are present, resulting in a reduction in pup weight gain in this context. Males appear to adjust their contributions to chasing in light of this cost, chasing at lower rates when their group contains dependent young. Our findings support the view that investment in cooperative behaviours can be attributed to benefits and costs, and highlight the additional importance of considering trade-offs in investment between cooperative behaviours.

## **5.2 Introduction**

Group living species often defend territories and the resources within them from intrusions by conspecific rivals (e.g., Packer et al. 1990; Baker and Dietz 1996; Boydston et al. 2001), with individual group members often differing markedly in their contributions (e.g., Heinsohn et al. 1996; Kitchen et al. 2004). Differential benefits may play a key role in mediating these differences in contributions to territory defence: territorial intruders are often in search of breeding opportunities (Møller 1987) and consequently, aggression by resident individuals towards intruders is typically sex-specific (Cant et al. 2002) and can be influenced by social status, which may determine access to breeding opportunities (e.g., O'Riain and Jarvis 1997; Cooney 2002). Few studies, however, have considered the likely additional importance of the costs of territorial defence for understanding individual differences in investment (Nunn 2000). Repelling intruders is expected to entail risk to self and energetic costs (e.g., Grinnell et al. 1995; Lazaro-Perea 2001; Kitchen et al. 2004), but may also entail more complex costs through trade-offs with other key behaviours (e.g., parental care: Wingfield et al. 1990). Nevertheless, few studies have actually quantified the costs of territorial behaviours (Myserud et al. 2004; Low 2006; Viera et al. 2011). Measuring these costs along with the benefits should help to advance our

understanding of the causes of individual differences in cooperative contributions to territory defence (Heinsohn and Packer 1995; Nunn 2000).

While the costs of repelling intruders may be determined primarily by the level of investment in high-energy or high-risk territorial behaviours (e.g., chasing and fighting: Grinnell et al. 1995; Lazaro-Perea 2001; Low 2006), the negative effects of territorial intrusions may be widespread across the group. The presence of territorial intruders can be disruptive to normal group activities, with resident individuals engaging in low-risk territorial behaviours at times when they might otherwise have been foraging (Boydston et al. 2001; Wilson et al. 2001; Jordan et al. 2007). In addition, as many territorial intrusions occur during the breeding season (Møller 1987), investment in territorial behaviours may come at the expense of investment in activities related to the rearing of young (Wingfield et al. 1990). Measuring these potential effects of the presence of territorial intruders, in terms of individual changes in body mass and contributions to the care of dependent young, is essential for understanding the overall costs of repelling intruders, both in the short and long term. Our limited understanding of costs of this kind are doubtless due in part to the difficulties of observing and identifying individual group members during interactions with intruders in the wild (Wingfield and Lewis 1993; Cant et al. 2002), and simultaneously monitoring changes in state and contributions to care.

In this study, we investigate individual variation in contributions to territorial defence and quantify both its benefits and costs in the cooperatively breeding meerkat, and consider the extent to which these benefits and costs appear to have shaped the patterns of contributions observed. Meerkats live in groups of up to 50 individuals, where a single, typically unrelated, dominant pair largely monopolizes within-group reproduction and close inbreeding is avoided (O'Riain et al. 2000; Spong et al. 2008). Dispersal is delayed beyond the age of sexual maturity in both males and females, who remain in their natal groups as subordinate helpers (Clutton-Brock et al. 2002; Russell et al. 2007), but subordinate males conduct extraterritorial prospecting forays throughout the breeding season (Young et al. 2007). Prospecting males regularly approach foreign groups and attempt to mate with dominant and subordinate females, which can lead to appreciable levels of extra-group paternity (Young et al. 2007; Spong et al. 2008). These events may not only reduce dominant male reproductive success (Spong et al. 2008), but also increase reproductive conflict

between dominant and subordinate females, as subordinates typically lack unrelated breeding partners in their natal group (O'Riain et al. 2000). Prospecting males have also been reported to take over established breeding groups (Doolan and Macdonald 1996b; Spong et al. 2008) and previous studies suggest that resident males respond aggressively to intrusions by prospectors (Doolan and Macdonald 1996b; Young et al. 2005; Mares et al. 2011). However, the factors that affect individual contributions to prospector repulsion have yet to be investigated, the benefits of such behaviour remain poorly understood and its costs are entirely unexplored.

Since prospectors typically approach groups that are actively foraging, territorial behaviours by residents may be expected to affect energy expenditure and reduce the time individuals are able to spend foraging. However, if the presence of prospecting males is disruptive to a group's overall investment in foraging, reductions in time spent foraging and, consequently, lower weight gain rates, may extend to the whole group. Meerkat pups start foraging with the group when they are about 30 days old, but remain nutritionally dependent on food from older group members until approximately 90 days of age (Brotherton et al. 2001). Whether investment in the repulsion of prospectors generates additional costs by trading off against contributions to care, as has been suggested to occur in birds (Wingfield et al. 1990), is as yet unknown.

Here, we first investigate the patterns of individual contributions to prospector repulsion through the leading of chases of intruding males. Second, we investigate the benefits of investing in prospector repulsion, focusing specifically on the benefits for residents of averting prospector immigrations (takeovers) in terms of the maintenance of group membership and social status. Third, we explore the potential short term costs of repelling prospectors, by measuring the effect of prospector presence on individual rates of weight gain and contributions to feeding dependent young. We then consider the extent to which these benefits and costs appear to have shaped the observed patterns of contributions to prospector repulsion.

## 5.3 Methods

### 5.3.1 Study population and general data collection

The study was conducted at the Kuruman River Reserve (26°59' S, 21°50' E) and surrounding ranch land in the southern Kalahari desert, South Africa. Details on climate and habitat at the study site are described elsewhere (Russell et al. 2002). The meerkats in our study population were habituated to close observation (within 2 m) and individually identifiable by unique dye marks on their fur. Groups were visited at least once every three days from 1998 to 2009 as part of a long-term study and life history events such as birth, emigration, immigration and changes in dominance were known almost to the day. Most individuals were weighed during these visits, once in the morning before the group started foraging and again 2 – 4 h later, covering the period when individuals typically gain the most weight (Turbé 2006). Individuals were trained to step on an electronic balance for small rewards of water or crumbs of hard boiled egg, which allowed us to record body mass to an accuracy of 1 g.

Body mass measurements taken in the mornings between 1998 and 2009 were used to estimate the age-corrected body mass of individuals included in our analyses (details below). We obtained a predicted body mass at each age in days for each individual from a biphasic growth model (English et al. 2011), using body mass records from 1064 individuals ( $n = 280260$  records of body mass), excluding measurements from females in the latter stages of pregnancy ( $< 40$  days to parturition or abortion; S. Sharp and T. Clutton-Brock, unpublished manuscript). We then subtracted the mean mass across all individuals for a given age to obtain age-corrected body mass. Predicted measures were used instead of actual mass records, as body mass records obtained in the field were not available for every day and the former allowed us to obtain mean measures that excluded seasonal fluctuations (English et al. 2011).

In all our analyses, individuals were assigned into age categories (Clutton-Brock et al. 2002) as follows: pup ( $< 91$  days of age), juvenile (91 – 180 days of age), subadult (181 – 360 days of age), yearling (361 – 720 days of age) and adult ( $> 720$  days of age). Adults were either dominant or subordinate, with all other age categories including only subordinate individuals (rare cases when a yearling was dominant were

excluded from our analyses). Dominant and subordinate individuals were distinguished behaviourally, as subordinate individuals are submissive to the dominant individual of the same sex (Carlson et al. 2004).

We used monthly measures of total rainfall in our analyses as a proxy for food availability (Cumming and Bernard 1997; Doolan and Macdonald 1997). Monthly rainfall was estimated using daily measures obtained from the Tropical Rainfall Measuring Mission data set, using the National Aeronautics and Space Administration's Goddard Earth Sciences Data and Information Services Center Interactive Online Visualization AND aNalysis Infrastructure (Giovanni; <http://disc.sci.gsfc.nasa.gov/giovanni>).

### **5.3.2 General statistical methods**

All statistical analyses were conducted using R (version 2.13.1; R Development Core Team 2011) with lme4 (version 0.999375-40; Bates et al. 2011) and glmmADMB (version 0.6.4; Skaug et al. 2011) for building linear mixed models (LMM) and generalized linear mixed models (GLMM). Model selection and comparison (see details below) were achieved using Akaike's information criterion values (AIC; Akaike 1973), corrected for small sample sizes (AICc; Burnham and Anderson 2002). We calculated the AICc differences ( $\Delta_i$ , the model's AICc minus the minimum AICc among candidate models) for each model and considered those with  $\Delta_i$  less than two to be the 'best', opting for simpler models (those with fewer estimated parameters) when more than one model had  $\Delta_i < 2$  and similar fits to the data in terms of log-likelihood (Burnham and Anderson 2002). Continuous input variables were standardized by subtracting the mean and dividing by two standard deviations (SD) to allow the comparison of their estimated effect sizes with those of binary and categorical predictors and facilitate the interpretability of interactions (Gelman and Hill 2007; Schielzeth 2010).

### **5.3.3 Investment in repelling prospectors**

In order to determine levels of investment in repelling prospecting males by resident individuals, we conducted behavioural observations at groups when prospectors were present, during the 2008 and 2009 breeding seasons (September – February). We

conducted a total of 62 observation sessions ( $\bar{x}$  = 80 min of observation time, SD = 27) across 11 groups and recorded *ad libitum* each time a prospector was chased by residents, noting the identity of individuals that led chases. A chase was defined as one or more resident individuals charging more than 2 m towards a prospector, which always resulted in the prospector fleeing. Chases led by individuals less than six months old were extremely rare (1% of chases) and were excluded from our analyses.

We first measured the overall difference between resident males and females in proportions of chases led. The total number of chases led by individuals of each sex (numerator) and the total number of chases recorded per observation session (denominator) were fitted as the proportional response variable in binomial GLMMs with logit link function. Chases led by each sex were entered separately into the model, as a single chase could be led by both female and male residents. Group identity was fitted as a random term in all candidate models (table A2.1) that included different combinations of the following input variables: sex, number of prospectors present at the group ( $\bar{x}$  = 2 prospectors, SD = 1), whether or not there were pups foraging with the group and the number of resident individuals over 180 days old (group size;  $\bar{x}$  = 14 individuals, SD = 5).

A second set of GLMMs was used to determine individual differences among males in the rate at which they led chases (females were excluded given the few chases they led, see results). We fit the number of chases per observation session as the response variable in negative binomial GLMMs that accounted for the duration of the session ( $\bar{x}$  = 81 min of observation time, SD = 26). The candidate models (table A2.2) included individual and group identities ( $n$  = 80 individuals in 10 groups) as random terms and different combinations of the following input variables: age category, age-corrected body mass ( $\bar{x}$  = 0.7 g, SD = 51.3) and social status of the resident individual, as well as the group size ( $\bar{x}$  = 15 individuals > 180 days old, SD = 5), whether or not there were pups foraging with the group and the number of prospectors present ( $\bar{x}$  = 2 prospectors, SD = 1).

#### 5.3.4 Benefits of averting prospector takeovers

To determine the effects of prospecting male immigrations on resident individuals' social status and group membership, we measured changes in group composition a week after an immigration event. We considered all cases when foreign males

immigrated into groups with a breeding hierarchy of adult females and one or more adult males (regardless of social status) from 12 years of field observations (1998 – 2009;  $n = 27$  groups where immigrations occurred). We restricted our analysis to the fates of individuals over six months old, based on minimum ages for breeding attempts of both males (observed prospecting or mating) and females (observed mating or pregnant). If resident dominants ( $n = 27$  females and 10 males) remained in their group after the immigration event, we assessed whether or not they maintained their social status up to three months after the event. We compared the number of individuals of each sex permanently leaving or losing dominance after an immigration event to those remaining with unaffected social status by means of a Fisher's exact test.

### 5.3.5 Costs of repelling prospectors

*Effects of prospectors on the weight gain rates of residents.* We compared the rates of weight gained by resident individuals on mornings when foreign males were prospecting at the group to the rates on mornings when there were no prospectors (within  $\pm 14$  days of the prospecting event), to determine the effect of the presence of prospectors. Rates of weight gain (g/h) were estimated using body mass measurements taken in the mornings before individuals started foraging and again 2 – 4 h later ( $\bar{x} = 198$  min), collected between 2000 and 2009 from 15 groups. These rates (difference in mass divided by time elapsed between measurements) were fitted as the response variable in a set of LMMs that included individual identity and observation session ( $n = 438$  individuals in 273 sessions) as random terms. Our candidate models (table A2.3) included different combinations of the following input variables: age category, age-corrected body mass ( $\bar{x} = -12$  g,  $SD = 60.3$ ) and social status of the resident individual, as well as the group size ( $\bar{x} = 26$  individuals  $> 90$  days old,  $SD = 9.6$ ), total rainfall in the past month ( $\bar{x} = 6$  mm,  $SD = 11.1$ ) and whether a prospector was present at the group or not. Given our expected results, we conducted separate models for males and females to avoid having to interpret complicated three-way interactions which could potentially be driven by the strong effect of sex. Groups with pups (either foraging or at the burrow) and females in the latter stages of pregnancy ( $< 40$  days to parturition or abortion), were excluded from our analysis to ease the interpretation of our results, as both factors are expected to



highly influence rates of weight gain (Clutton-Brock et al. 1998b; Clutton-Brock et al. 2002; S. Sharp and T.H. Clutton-Brock, unpublished manuscript).

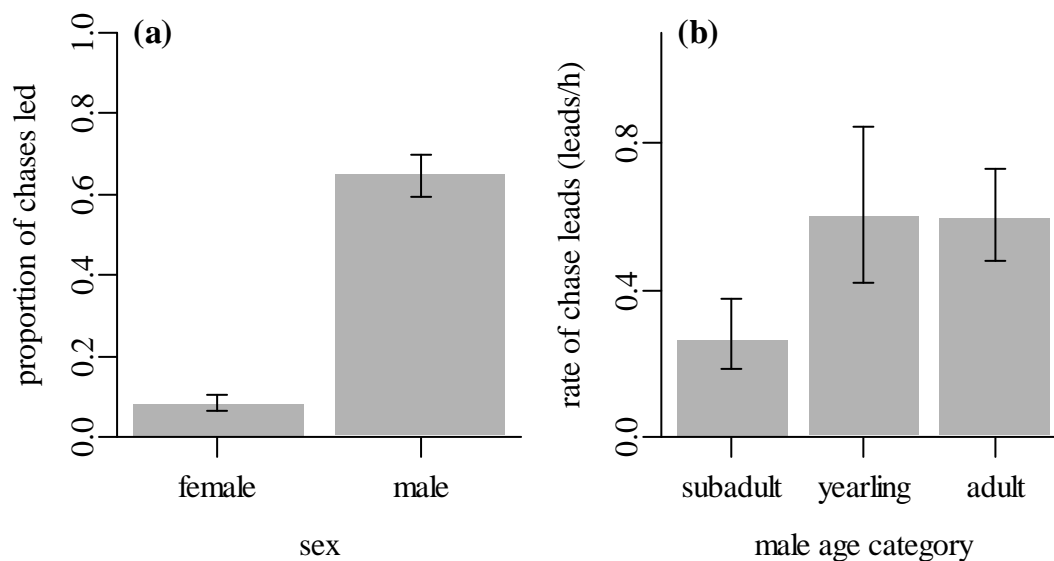
*Effects of prospectors on the pup feeding rates of residents.* We compared individual rates of pup feeds on mornings when foreign males were prospecting at the group to the rates on mornings when there were no prospectors (within  $\pm 14$  days of the prospecting event), to determine the effect of the presence of prospectors. Pup feeds per individual were collected *ad libitum* while groups were foraging with pups between 2000 and 2009 (Brotherton et al. 2001;  $n = 14$  groups). The number of feeds was fitted as the response variable in negative binomial GLMMs that included individual identity and observation session ( $n = 440$  individuals in 393 sessions) as random terms and accounted for the duration of each session ( $\bar{x} = 170$  min,  $SD = 22.9$ ). Our candidate models (table A2.4) included different combinations of the following input variables: number of pups foraging with the group ( $\bar{x} = 4$  pups,  $SD = 1.7$ ), modal pup age ( $\bar{x} = 59$  days old,  $SD = 16.9$ ), group size ( $\bar{x} = 20$  individuals  $> 90$  days old,  $SD = 7.3$ ), total rainfall in the past month ( $\bar{x} = 19$  mm,  $SD = 20.2$ ) and whether a prospector was present at the group or not. As sex is known to have a strong effect on pup feeding rates (Clutton-Brock et al. 2002), we conducted separate models for males and females as above, to ease the interpretation of our results.

*Effects of prospectors on the weight gain rates of pups.* Using the method described for our analysis on weight gain rates and body mass records from the foraging sessions in the pup feed analysis, we determined whether pups also gained less weight per hour when prospectors were present than when absent. Our candidate LMMs (table A2.5) included group and pup identities as random terms and different combinations of the following input variables: number of pups foraging with the group ( $\bar{x} = 4$  pups,  $SD = 1.8$ ), pup age ( $\bar{x} = 62$  days old,  $SD = 16.9$ ), group size ( $\bar{x} = 15$  individuals  $> 90$  days old,  $SD = 6.2$ ), total rainfall in the past month ( $\bar{x} = 24$  mm,  $SD = 22.6$ ) and whether a prospector was present at the group or not.

## 5.4 Results

### 5.4.1 Investment in repelling prospectors

Chases were typically led by a single resident individual (range one to three leaders;  $n = 344$  chases of which 234 had a single clear leader) who usually chased on its own. Males led a much higher proportion of chases than females (best GLMM in table A2.1: effect of sex  $\pm$  standard error (SE) =  $3.01 \pm 0.22$ ,  $z = 13.77$ ,  $P < 0.001$ ; figure 5.1a). Within males, age-corrected body mass had a positive effect on the rate of chase leads, the presence of pups had a negative effect and adults led chases at higher rates than subadults (table 5.1; figure 5.1b). Including a male's social status (table A2.2) did not produce models with better fits than the model in table 5.1, indicating that there was no difference in the rates of chase leads between dominant and subordinate males of the same age category.



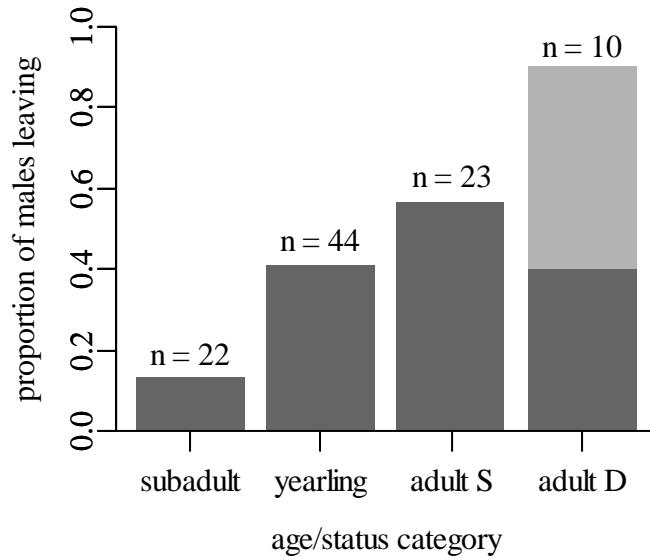
**Figure 5.1:** Effects of (a) sex on the proportion of chases led out of the total number of chases of prospectors recorded per observation session; and of (b) age category on the rate at which resident males led chases (leads/h). Proportions in (a) do not add to one because leaders were not identified in all of the chases recorded. Predictions were estimated from the best GLMM in table A2.1 for (a) and the GLMM in table 5.1 for (b), using means of predictors not graphed. Error bars are prediction intervals (SE) accounting for the uncertainty in the estimates of the fixed effects.

Fixed terms	Estimate $\pm$ SE	<i>z</i>	<i>P</i>
(Intercept)	-4.62 $\pm$ 0.21	-22.23	
Age category			< 0.001
Subadult	-0.80 $\pm$ 0.25	-3.21	
Yearling	-0.00 $\pm$ 0.26	-0.03	
Body mass adjusted for age	0.49 $\pm$ 0.22	2.20	0.022
Pups foraging (yes)	-0.46 $\pm$ 0.20	-2.33	0.019
Group size * No. of prospectors	-1.91 $\pm$ 0.47	-4.09	< 0.001
Group size	-0.74 $\pm$ 0.21	-3.47	
No. of prospectors	-0.47 $\pm$ 0.22	-2.14	

**Table 5.1:** Factors influencing the rate at which resident males led chases of prospectors. Results from the best GLMM ( $n = 402$  observations) in table A2.2 with negative binomial error structure, and with group ( $n = 10$  groups; variance = 0.00) and individual ( $n = 80$  individuals; variance = 0.07) identities as random terms. Estimates for continuous fixed terms were calculated from standardized input variables.

#### 5.4.2 Benefits of averting prospector takeovers

Resident males were more likely than females to be affected by the immigration of a prospecting male within the first week of the event (18 groups where males lost dominance or emigrated and only two where females disappeared, out of 27 groups; Fisher's exact test:  $P < 0.001$ ). Nine males lost dominance (including four that left) and 34 subordinate males left their groups permanently within a week after a prospector immigration event, with all dominant males ultimately leaving over the next three months ( $n = 10$  dominant and 89 subordinate males; not all groups had a dominant male before the event). Only two subordinate females disappeared from their groups within the first week of the arrival of a new male and one female lost dominance to a subordinate in her group during the next three months ( $n = 27$  dominant and 118 subordinate females). Within males, subadults were the least likely to be affected by prospector immigrations (figure 5.2).



**Figure 5.2:** Proportion of males in each age and social status category (S, subordinate; D, dominant) that permanently left their group (dark grey) or stayed but lost dominance (light grey), within the first week after a prospecting male immigrated into their group ( $n = 27$  immigration events).

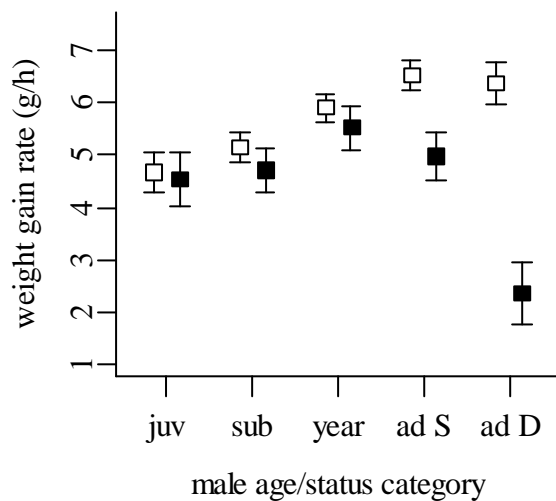
#### 5.4.3 Costs of repelling prospectors

*Effects of prospectors on the weight gain rates of residents.* The presence of prospecting males affected weight gain rates of both dominant and adult subordinate males. Rates of weight gain for dominant males dropped by more than 60% and by over 20% for adult subordinates, when prospectors were present at the group (figure 5.3), after controlling for total rainfall in the past month (table 5.2a). The weight gain rates of younger males were also reduced in the presence of prospectors, but to a much lesser extent (figure 5.3). The rates of weight gain of females, by contrast, were not affected by the presence of prospectors in any age or status category (table 5.2b).

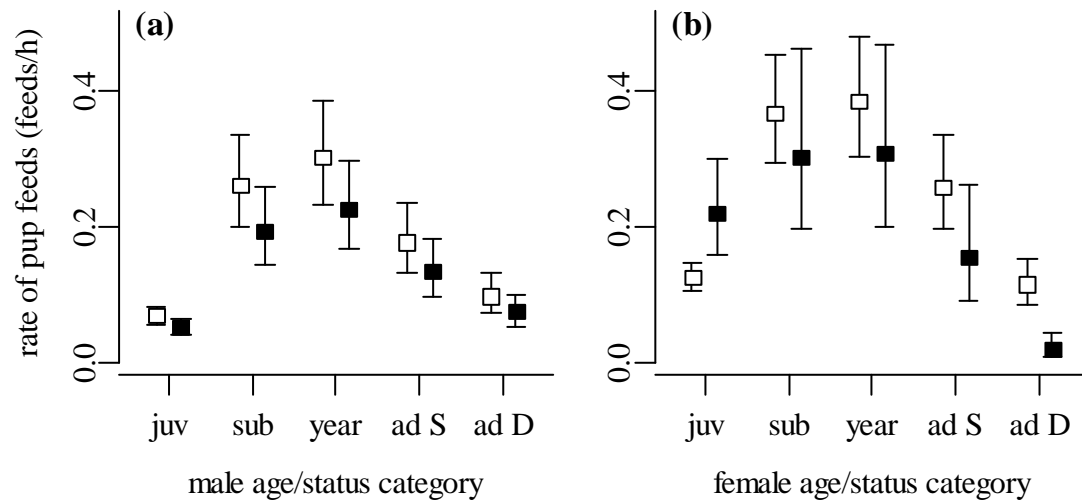
*Effects of prospectors on pup feeding rates of residents.* The rates at which males and females fed pups were affected by the presence of prospectors (table 5.3). After controlling for the number of pups foraging with the group, modal pup age, group size and total rainfall in the past month, males across all age and status categories fed pups at lower rates when prospecting males were present at the group than when there were no prospectors (table 5.3a; figure 5.4a). Females in most age categories also reduced their rates of pup feeds in the presence of prospectors, with dominants lowering their

rates by 50% (table 5.3b; figure 5.4b). By contrast, juvenile females showed a considerable increase in pup feeding rate (figure 5.4b).

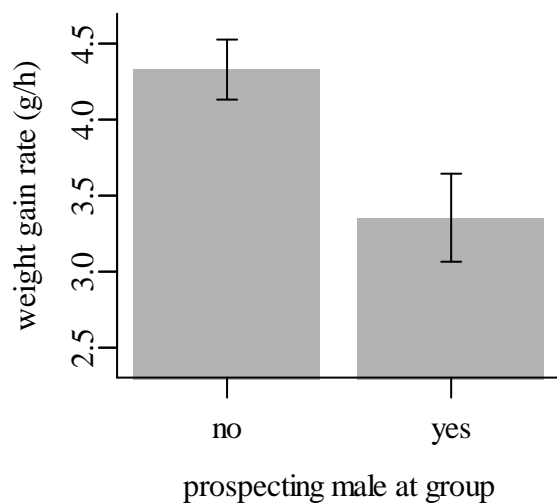
*Effects of prospectors on the weight gain rates of pups.* Within these same observation sessions, pups gained considerably less weight per hour of foraging when prospectors were present than when they were not (figure 5.5), after controlling for the effects of pup age and number, and the total rainfall in the past month (table 5.4).



**Figure 5.3:** Effect of the interaction between the presence of a prospector (open: absent; solid: present) and the age and social status category (S, subordinate; D, dominant) on rates of weight gain (g/h) of resident males. Predictions were estimated from the LMM in table 5.2a using means of predictors not graphed. Error bars are prediction intervals (SE) accounting for the uncertainty in the estimates of the fixed effects.



**Figure 5.4:** Effect of the presence of prospectors (open: absent; solid: present) on pup feed rates (feeds/h) of (a) males and (b) females (including interaction with age and status category: S, subordinate; D, dominant). Predictions were estimated from the GLMMs in table 5.3a for (a) and table 5.3b for (b), using means of predictors not graphed. Error bars are prediction intervals (SE) accounting for the uncertainty in the estimates of the fixed effects.



**Figure 5.5:** Effect of the presence of prospectors at the group on weight gain rates (g/h) of pups. Predictions were estimated from the LMM in table 5.4, using means of predictors not graphed. Error bars are prediction intervals (SE) accounting for the uncertainty in the estimates of the fixed effects.

Response term	Fixed terms	Estimate $\pm$ SE	<i>t</i>	<i>P</i>
(a) Male	(Intercept)	4.68 $\pm$ 0.38	12.39	
weight gain	Rainfall in past month <sup>2</sup>	-1.18 $\pm$ 0.28	-4.28	< 0.001
rate (g/h)	Rainfall in past month	3.43 $\pm$ 0.59	5.86	
	Age/status category * Prospector (yes)			< 0.001
	Subadult * Prospector	-0.29 $\pm$ 0.58	-0.50	
	Yearling * Prospector	-0.23 $\pm$ 0.58	-0.40	
	Adult Subordinate * Prospector	-1.40 $\pm$ 0.61	-2.29	
	Adult Dominant * Prospector	-3.89 $\pm$ 0.75	-5.18	
	Age/status category			
	Subadult	0.47 $\pm$ 0.36	1.29	
	Yearling	1.22 $\pm$ 0.36	3.39	
	Adult Subordinate	1.85 $\pm$ 0.38	4.90	
	Adult Dominant	1.69 $\pm$ 0.48	3.55	
	Prospector (yes)	-0.15 $\pm$ 0.61	-0.24	
(b) Female	(Intercept)	6.30 $\pm$ 0.27	23.28	
weight gain	Rainfall in past month <sup>2</sup>	-0.84 $\pm$ 0.23	-3.60	< 0.001
rate (g/h)	Rainfall in past month	3.36 $\pm$ 0.54	6.19	
	Age category			< 0.001
	Juvenile	-2.02 $\pm$ 0.32	-6.35	
	Subadult	-1.60 $\pm$ 0.28	-5.68	
	Yearling	-1.20 $\pm$ 0.25	-4.85	
	[Prospector]			[0.938]
	[Age category * Prospector]			[0.870]

**Table 5.2:** Factors affecting the rate of weight gain (g/h) of resident (a) males and (b) females. Results from the best LMMs in table A2.3. For (a) males ( $n = 2177$  observations) and (b) females ( $n = 1749$  observations), observation session ( $n = 273$  and  $272$  sessions; variances =  $7.28$  and  $5.92$ , respectively) and individual identity ( $n = 229$  males and  $209$  females; variances =  $0.71$  and  $0.78$ , respectively) were fitted as random terms. Predictors in brackets in (b) were not included in the best model and are presented for comparative purposes only. Estimates for continuous fixed terms were calculated from standardized input variables.

Response term	Fixed terms	Estimate $\pm$ SE	$z$	$P$
(a) Male	(Intercept)	-6.78 $\pm$ 0.19	-35.44	
pup feed rate	Number of pups	0.23 $\pm$ 0.10	2.21	0.027
(feeds/h)	Modal pup age <sup>2</sup>	-1.69 $\pm$ 0.22	-7.65	< 0.001
	Modal pup age	-0.55 $\pm$ 0.10	-5.24	
	Group size	-0.87 $\pm$ 0.12	-7.11	< 0.001
	Rainfall in past month	0.53 $\pm$ 0.10	5.37	< 0.001
	Age/status category			< 0.001
	Subadult	1.34 $\pm$ 0.19	7.18	
	Yearling	1.48 $\pm$ 0.19	7.94	
	Adult Subordinate	0.96 $\pm$ 0.20	4.85	
	Adult Dominant	0.35 $\pm$ 0.23	1.53	
	Prospector (yes)	-0.29 $\pm$ 0.12	-2.51	0.012
(b) Female	(Intercept)	-6.19 $\pm$ 0.17	-36.93	
pup feed rate	Modal pup age <sup>2</sup>	-1.77 $\pm$ 0.22	-7.99	< 0.001
(feeds/h)	Modal pup age	-0.60 $\pm$ 0.10	-5.81	
	Group size	-0.75 $\pm$ 0.12	-6.35	< 0.001
	Age/status category * Prospector (yes)			< 0.001
	Subadult * Prospector	-0.76 $\pm$ 0.27	-2.88	
	Yearling * Prospector	-0.80 $\pm$ 0.26	-3.09	
	Adult Subordinate * Prospector	-1.09 $\pm$ 0.34	-3.26	
	Adult Dominant * Prospector	-2.43 $\pm$ 0.65	-3.77	
	Age/status category			
	Subadult	1.09 $\pm$ 0.16	6.71	
	Yearling	1.13 $\pm$ 0.16	6.98	
	Adult Subordinate	0.74 $\pm$ 0.19	3.85	
	Adult Dominant	-0.07 $\pm$ 0.22	-0.32	
	Prospector (yes)	0.57 $\pm$ 0.25	2.25	

**Table 5.3:** Factors affecting the rates of pup feeds (feeds/h) for (a) males and (b) females. Results from the best GLMMs with negative binomial error structure in table A2.4. For (a) males ( $n = 3348$  observations) and (b) females ( $n = 2782$  observations), observation session ( $n = 393$  sessions; variances = 0.52 and 0.50, respectively) and individual identity ( $n = 230$  males and 210 females; variances = 0.30 and 0.21, respectively) were fitted as random terms. Estimates for continuous fixed terms were calculated from standardized input variables.



Fixed terms	Estimate $\pm$ SE	<i>t</i>	<i>P</i>
(Intercept)	5.16 $\pm$ 0.37	14.02	
Prospector (yes)	-0.96 $\pm$ 0.27	-3.54	< 0.001
Pup age	1.30 $\pm$ 0.24	5.45	< 0.001
Number of pups	-0.20 $\pm$ 0.08	-2.59	0.009
Rainfall in past month	1.29 $\pm$ 0.25	5.14	< 0.001

**Table 5.4:** Factors affecting the rates of weight gain (g/h) of pups. Results from the best LMM in table A2.5 ( $n = 572$  observations) fitted with group ( $n = 14$  groups; variance = 0.26) and individual ( $n = 151$  pups; variance = 0.05) identities as random terms. Estimates for continuous fixed terms were calculated from standardized input variables.

## 5.5 Discussion

Our findings suggest that patterns of individual contributions to cooperative territory defence can be attributed to variation in both the benefits and costs of territorial behaviours, and highlight the potential importance of considering trade-offs in investment between cooperative behaviours. Males invest substantially more than females in repelling prospectors, reflecting the benefits of keeping prospectors at bay: males lost dominance and were likely to be expelled from their groups following prospector immigrations, whereas females were not affected by prospector takeovers. However, territorial defence is likely to be costly, as suggested by the reduction in weight gain for males, but not females, in the presence of prospectors. Accordingly, males that were heavier for their age were able to invest more in leading chases of prospectors. We also show evidence of a wider cost of conflict with extra-group individuals, not restricted to those individuals engaged in chasing: both males and females reduced their cooperative contributions to pup feeding when prospectors were present, resulting in a marked reduction in pup weight gain in this context. This finding suggests a trade-off between investment in cooperative territorial defence and cooperative care of young. Indeed, males appeared to adjust their cooperative contributions to chasing in light of this cost, leading chases at lower rates when their group contained dependent young.

Dominant male meerkats may lose substantial fitness to prospecting males through reductions not only in current (Young et al. 2007; Spong et al. 2008), but also future reproductive success when prospector intrusions and immigrations are

successful. Although we did not directly observe males being expelled from their groups during takeovers, nine of the resident males that lost dominance (including those that permanently left) were unrelated to the dominant female and therefore, unlikely to have left voluntarily (Griffin et al. 2003; Young et al. 2007; Spong et al. 2008). Extra-group male takeovers leading to evictions or even death of resident breeding males have been reported in a number of species where males fiercely defend their territory and mates (e.g., lions: Grinnell et al. 1995; golden lion tamarins: Baker and Dietz 1996). Given that the probability of becoming a dominant male breeder is low and that reproductive success as a dominant is dependent on tenure length (Clutton-Brock et al. 2006; Spong et al. 2008), repelling prospectors as a way of defending the dominant position may be as important as its function in preventing female extra-group mating. These benefits of investing in territorial behaviours are likely to explain the high rates of chases led by dominant males.

Yearling and adult subordinate males were also expelled from their groups within the first week after the successful immigration of a prospecting male, despite the fact that 94% of those expelled were in their natal groups and hence would not have represented a threat to the within-group reproductive success of immigrant males (Griffin et al. 2003; Young et al. 2007; Spong et al. 2008). Similarly in lions, where inbreeding is also avoided (Packer et al. 1991), subadult males are evicted from their natal pride after the arrival of a new male (Hanby and Bygott 1987). The threat of losing the safe haven from which to conduct forays in search of mating and dispersal opportunities (Kokko and Ekman 2002), may explain why in meerkats, older subordinate males lead chases of prospectors at similar rates to those of dominants. Subordinate individuals of both sexes are also expected to gain greater indirect fitness benefits from helping to raise offspring fathered by the dominant male rather than extra-group males, as he is typically their own father (Griffin et al. 2003; Spong et al. 2008). By chasing prospectors, subordinates may therefore be exhibiting an aggressive form of ‘mother guarding’ (Welbergen and Quader 2006), while also contributing to secure their father’s tenure as the dominant breeder.

By contrast, the residency and social status of females is rarely affected by male takeovers, suggesting that, unlike males, females stand to gain little direct benefit from repelling prospectors. Indeed, subordinate females may gain direct benefits from tolerating the presence of prospectors by obtaining access to breeding

opportunities (Griffin et al. 2003; Spong et al. 2008) and, in the case of prospector takeovers, by having an unrelated resident male to partner them if they were to inherit dominance. These direct fitness benefits, coupled with the absence of a clear direct cost arising from male takeovers, most likely explain why females contribute substantially less than males to the repulsion of prospecting males. Furthermore, the energetic costs of territorial behaviours may outweigh any potential indirect fitness gain for subordinate females, as females in better condition are more likely to breed themselves (Clutton-Brock et al. 2008). Given that subordinate females are capable of breeding, it is perhaps surprising that the arrival of a new male did not lead to changes in dominance, as has been reported in other species where close inbreeding is avoided (e.g., Damaraland mole-rats: Cooney and Bennett 2000). Sharp and Clutton-Brock (2011) suggest that in meerkats, the probability of subordinate females successfully challenging the dominant female is extremely low and the cost of failure high. This lack of a threat to the dominant female's tenure may also explain why dominant females invest little in chasing prospectors.

The cost of repelling prospectors was clearly reflected in the changes in weight gain rates of residents in the presence of prospectors: males invest highly in chasing prospectors and suffered reduced weight gain rates, whereas females, who invest little in chasing, were unaffected by the presence of prospectors. These results are in line with what was found in stitchbirds, where male weight loss during the fertile period of their mate is associated with the effort invested in chasing intruding males (Low 2006). Although dominant males led chases at comparable rates to adult subordinates, they suffered substantially greater reductions in weight gain than subordinates, suggesting that they may engage in additional behaviours that detract from foraging during prospector intrusions. Probable increases in other previously reported territorial behaviours (e.g., scent marking: Doolan and Macdonald 1996b; Jordan et al. 2007; Mares et al. 2011) are likely to have contributed to the 60% reduction in weight gain rate observed in dominant males. Given that prospectors typically follow groups for entire days and visit the same groups repeatedly (Drewe et al. 2009), these short term reductions in weight gain among resident males could lead to significant weight loss over the entire breeding season, as has been shown in stitchbirds (Low 2006) and several ungulate species (Mysterud et al. 2004). Indeed, our findings suggest that males adjust their contributions to chasing so as to mitigate

this potential weight loss cost, as males that were heavier for their age contributed more to chasing than those that were light.

Our analyses also revealed evidence of a second cost associated with prospector repulsion, which was not restricted solely to those individuals engaged in chasing. In the presence of prospectors, both male and female group members fed dependent pups at lower rates, resulting in reduced overall rates of weight gain among the pups. Among males, this pattern could reflect an energetic trade-off between chasing and pup feeding, as contributions to pup feeding are state dependent (Clutton-Brock et al. 2001a; Clutton-Brock et al. 2002). A similar trade-off has been documented among prospecting male meerkats, with prospecting resulting in weight loss and elevated circulating testosterone levels (presumably due in part to their aggressive encounters at foreign groups), both of which could explain their reduced contributions to pup feeding on returning to their group (Young et al. 2005). Similar elevations in testosterone levels could also occur among resident males engaged in chasing these prospectors, and this too could account for their reduced rates of pup feeding (Wingfield et al. 1990; Hirschenhauser and Oliveira 2006). As females chase prospectors markedly less frequently than males, however, it is perhaps surprising that they too show a clear reduction in pup feeding rates comparable to that observed in males. An as yet unexplored possibility is that a sudden increase in subordinate breeding opportunities intensifies reproductive conflict between females and leads to increased aggression (Emlen 1995; Cooney and Bennett 2000).

While young females appear to partially compensate for the reductions in the pup feeding rates of others when prospectors are present by increasing their own rates, pups still experienced an overall reduction in their rates of weight gain when prospectors were present. Although we have only measured the short term effects on pup body mass, these reductions in weight gain could have long term effects if they occur frequently over the breeding season, as pups in better body condition develop greater foraging efficiency and have a higher probability of gaining reproductive success as adults (Russell et al. 2007; Thornton 2008). To our knowledge, this is the first study to demonstrate effects of intrusions on contributions to cooperative care, findings that are suggestive of a trade-off in investment between cooperative behaviours. Indeed, our findings suggest that cooperative contributions to chasing are

adjusted so as to minimize this net cost of chasing, as males were less likely to lead chases when dependent pups were foraging with their group.

In conclusion, dominant and older subordinate male meerkats seem to cooperate in territorial defence by chasing intruders. By repelling prospectors, dominant males may secure their top breeding position and reproductive success, males in general secure their group membership, and subordinates gain indirect fitness benefits from assisting in this regard. However, territorial defence appears to be costly, as shown by the reduction in weight gain among males, but not females, in the presence of prospectors. The negative effects of male territorial intrusions also extend to pup weight gain, as feeding rates across individuals of both sexes were reduced in the presence of prospectors. Both these benefits and costs of prospector repulsion appear to have shaped the patterns of cooperative contributions to territorial defence, as males contributed substantially more than females, did so in a condition-dependent manner and tempered their chasing when simultaneously feeding dependent young. Further research is warranted to explore the long term consequences of repeated territorial intrusions for both adult male and pup weight gain and to investigate why females reduce their pup-feeding rates rather than offset male reductions in care in the presence of prospectors. Together our findings support the view that variation in individual contributions to cooperative behaviour can be attributed to variation in both its benefits and costs, and highlight the additional importance of considering trade-offs in investment between different cooperative behaviours.



## CHAPTER 6

### **Responses to intruder scents: sex and social status differences and temporal variation**

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*Note:* This chapter was published as Mares, R., A. J. Young, D. L. Levesque, N. Harrison, and T. H. Clutton-Brock. 2011. Responses to intruder scents in the cooperatively breeding meerkat: sex and social status differences and temporal variation. *Behavioral Ecology* 22:594–600. I designed the experiment; Danielle Levesque, Nicola Harrison and I conducted the experiment; and Andrew Young and Tim Clutton-Brock contributed to discussion. I analysed the data and wrote the paper.

## 6.1 Abstract

While sex-specific responses to intruder scent marks have been described in many mammal species, less is known about variation in responses in cooperatively breeding species where differential access to breeding opportunities exists within groups. When reproductive skew is high, strong responses to extra-group breeding rivals would be expected mainly from dominant individuals, with levels of investment depending on female receptiveness. However, evidence from controlled experiments on cooperative breeders for sex and social status differences in responses to intruder scent marks is limited. Here, we investigated responses to intruder scent marks in cooperatively breeding meerkats, where a single dominant pair largely monopolizes within-group reproduction. A series of experimental presentations using faeces were used to test first, whether meerkats discriminate between resident and extra-group male scent marks; second, whether sex and social status affects the response to intruding male scents; and third, whether dominant males increase their level of response when dominant females are most receptive. Our results suggest that meerkats are able to discriminate between resident and intruding male scent marks, and show that dominant males have the strongest overall response to intruder scent marks which does not increase with female receptiveness. We suggest that, although all group members may be affected by the presence of intruders, reproductive conflict may be the main reason for the stronger response of dominant males to extra-group male scent marks in this cooperatively breeding species with high reproductive skew.

## 6.2 Introduction

Scent-marking plays a fundamental role in communication in many mammal species, allowing information such as the species, sex, individual identity, health and reproductive status of a signaller to persist in the environment (Wyatt 2003; Johansson and Jones 2007). This information may advertise competitive abilities (Hurst and Beynon 2004), thus scent-marking with urine, faeces and scent gland secretions has traditionally been associated with territoriality and resource defence (Gosling and Roberts 2001). Resource holders tend to scent-mark more than others



and, in territorial species, they respond to scent marks of intruding individuals in ways that reflect the level of threat posed by the intruder (Johnson 1973; Gosling and Roberts 2001; Hurst and Beynon 2004). Strong intrasexual competition over resources such as food, shelter and mates (Boydston et al. 2001; Cant et al. 2002) therefore, predicts that individuals will respond most aggressively towards scent marks of intruders of the same sex (Gosling and Roberts 2001; Palagi and Dapporto 2007). In gregarious species, cooperative resource defence among same-sex individuals is fairly common (e.g., lion: Heinsohn et al. 1996; common marmoset: Lazaro-Perea 2001; chimpanzee: Wilson et al. 2001), yet differences in social status may also affect responses to intruders (e.g., naked mole-rat: O'Riain and Jarvis 1997; Damaraland mole-rat: Cooney 2002) and to their scent marks (reviewed in Thiessen and Rice 1976; e.g., house mouse: Hurst 1990).

In cooperatively breeding species, social status often determines access to breeding opportunities, and the distribution of reproduction within groups may affect whether breeding rivals come from within or outside the group. In the banded mongoose, a species with relatively low reproductive skew, males reflect competition for mates within their groups by selectively counter-marking male scent marks from their own group (Müller and Manser 2008). In contrast, when reproductive skew is high and breeding rivals are likely to come from outside the group, strong responses would be expected towards intruder scent marks, primarily from dominant individuals who have more to lose in terms of breeding opportunities. In addition, dominant males may vary their response depending on female receptiveness (Müller and Manser 2008). Constraints on subordinate dispersal and breeding, along with the indirect fitness benefits accrued through the reproduction of closely related breeders (Emlen 1991) may also lead to strong responses to intruders from subordinate individuals. To our knowledge, there are no controlled experiments investigating sex and social status differences in responses to intruder scent marks in cooperative breeders with high reproductive skew.

In this study, we investigated individual responses to intruder scent marks in meerkats, a cooperatively breeding species of mongoose that live in groups of up to 50 individuals, where a single dominant pair largely monopolizes within-group

reproduction (Griffin et al. 2003; Spong et al. 2008). Dominant individuals are typically unrelated to each other, and inbreeding with offspring and siblings that remain in the group as subordinate helpers is avoided (Spong et al. 2008). Ultimately, subordinates of both sexes may disperse from the natal group, but unlike females, males leave voluntarily and conduct extraterritorial prospecting forays prior to dispersal (Young et al. 2007). During these forays, prospectors regularly approach foreign groups and may mate with both dominant and subordinate females, leading to appreciable levels of extra-group paternity (Young et al. 2007; Spong et al. 2008). Prospecting male coalitions can also take over established breeding groups, ejecting all adult resident males in the process (Doolan and Macdonald 1996b; Young 2003). Previous studies suggest that resident males respond most aggressively to intrusions by prospecting males (Doolan and Macdonald 1996b; Young et al. 2005), yet a detailed analysis of the effects of sex and social status on the individual behavioural responses to prospectors has not been done.

Here, we investigated the responses of meerkats of different sex and social status to scent marks of prospecting males, as territorial intruders. Prospecting males regularly deposit faeces and anal marks (Jordan 2007) in conspicuous locations upon encountering foreign groups (R Mares, D Levesque, N Harrison, personal observation), presumably as a form of advertisement to potential mates. Previous studies on scent-marking behaviour in meerkats have focused on latrines, where both dominant and subordinate males scent-mark significantly more than females and over-mark female scent marks more frequently than those of other males from their own group (Jordan 2007). However, besides anecdotal evidence (Doolan and Macdonald 1996b; Manser 2001), it is unclear whether meerkats respond differently to extra-group scent marks than to those from their own group members. We therefore conducted a series of faecal presentation experiments on groups of wild meerkats to determine, first, whether meerkats respond differently to resident and extra-group subordinate male scent marks, and second, whether responses to extra-group scents differ between resident individuals of different sex or social status. We also investigated whether dominant males change their response to these foreign scent marks depending on the reproductive status of the resident dominant female. We predicted that all meerkats would have a distinct response to extra-group scent marks

compared to resident scents, and that there would be differential responses among individuals to extra-group scents according to threat. Given the greater risk of reproductive competition between intruding males and resident dominant males, compared to dominant females or subordinate individuals, we expected that dominant males would show the strongest response to intruding male scent marks. We also predicted that dominant males would further increase their level of response when resident dominant females were in oestrus.

## **6.3 Methods**

### **6.3.1 Study area and population**

The study was conducted on a wild population of meerkats at the Kuruman River Reserve (26° 59' S, 21° 50' E) and surrounding ranch land in the southern Kalahari desert, South Africa, during the 2008 and 2009 breeding seasons (September to February). Details on climate and habitat at the study site and female fertility patterns of the study population are described elsewhere (Russell et al. 2002; Young et al. 2007). The meerkats in the population are habituated to close observation (within 2 m), are individually identifiable by unique dye-marks on their fur and have known life histories, as groups are visited at least once every three days. Individuals are accurately categorized by social status as either dominant or subordinate, as subordinate individuals are behaviourally submissive to the dominant individual of the same sex in their group (Carlson et al. 2004).

### **6.3.2 Faecal sample collection and presentation**

Faeces from subordinate males were collected *ad libitum* immediately after deposition. Two thirds of each deposit were placed in individual plastic bags and put into a flask with ice, leaving the rest of the sample at its original location to avoid disrupting its potential communicative value. Samples were transferred to a freezer (-2 °C to -6 °C) within four hours of collection and kept frozen until 10 minutes prior to each presentation. Faecal samples were always presented individually and in random

order (see details below) to single individuals in the morning, when meerkat groups are actively foraging. Samples were put on a 20 x 30 cm tray that was covered with locally collected sand before each presentation and placed in the foraging path of the recipient individual. The response to the faecal sample was recorded with a digital video camera (NV-GS500, Panasonic Corporation, Japan) mounted on a tripod and positioned within one metre of the presentation tray. We filmed the recipient individual from the moment it entered the field of view of the camera (45 – 60 cm around the tray) and inspected the faecal sample, until it resumed foraging or left the field of view and did not return to inspect the sample again for one minute. In all of our experiments, recipient individuals were presented only once with each faecal sample type (see details below), and no more than two individuals per group were presented with samples within a same week to avoid habituation to the experiments.

### **6.3.3 Behavioural data collection**

We recorded the time recipient individuals spent inspecting the faecal sample (nose within 1 cm of the sample) and the number of recruitment calls (Manser 2001) emitted and counter-marks deposited in response to the sample. Counter-marking included: anal marking (wiping the anal region across a surface), chew marking (biting vegetation), scuffing (frenzied digging), urinating and defecating (Jordan 2007). We extracted the frequency and duration (to the nearest 0.02 s) of the behaviours of interest from the video recordings using the program fOCUS III (The Open University and Psycle Interactive, UK). In addition to the behaviours recorded in the presence of the faecal sample, we conducted 10 minute focal observations of the recipient individual after each presentation, once filming had concluded and the faecal sample had been removed. Time spent vigilant was recorded on a handheld computer (Organiser II LZ64, Psion Teklogix, UK), with times accurate to 1 s. Individuals were considered vigilant when they were bipedal or on raised guard (vigilant from a raised position, Clutton-Brock et al. 1999c), with their gaze at the horizon. For experiment II, we conducted an additional focal observation before each presentation as a control, and we also recorded the time spent within one metre of the dominant female, an indication of mate-guarding (Jordan et al. 2007). We used the

differences between post-presentation and control focal observation times in the analyses of these data.

#### **6.3.4 Experiment I – sex and social status differences in responses**

To determine first, whether meerkats respond differently to male scent marks from resident and foreign individuals (intruders), and second, whether dominant males show stronger responses to intruder scent marks than individuals in all other sex and social status categories, faecal samples from resident males and foreign males were presented to the dominant and one adult subordinate individual of each sex in eight meerkat groups. A sample from a randomly selected subordinate male from the recipient individual's own group, deposited while foraging with the group, was used as the resident sample. Foreign samples were collected from extra-group subordinate males while they were on prospecting forays. Potential differences among recipient individuals in their familiarity to the foreign sample donors were minimized by using faecal samples from males who themselves and their groups had not encountered the recipient individual or its group within six months prior to their presentation. Samples from resident and foreign males did not differ significantly in the number of days since their deposition at the time of presentation (resident:  $\bar{x} = 25$  days, range 3 – 76; foreign:  $\bar{x} = 35$  days, range 1 – 86; Wilcoxon signed-rank test:  $Z = -1.66$ ,  $P = 0.099$ ). Recipient individuals were presented with a sample of each type on the same day, with a one hour interval between presentations.

A second series of presentations was conducted separately to verify that responses to the foreign samples were due to the donors being from a different group to that of the recipient, rather than because the samples were collected while the donors were prospecting. An identical protocol was followed except that, in this case, the faecal sample deposited while prospecting was collected from a subordinate male from the recipient individual's own group. This same resident male also provided the control sample, but deposited while foraging with its group. Prospecting and control samples did not differ significantly in the number of days since their deposition at the time of presentation (prospecting:  $\bar{x} = 42$  days, range 13 – 60; control:  $\bar{x} = 41$  days, range 8 – 80; Wilcoxon signed-rank test:  $Z = 0.36$ ,  $P = 0.748$ ). Samples were

presented to the dominant male and one randomly selected subordinate male in each of five groups.

### **6.3.5 Experiment II – temporal variation in response by dominant males**

To determine whether dominant males increase their response to intruder scent marks when resident dominant females are in oestrus, faecal samples from foreign subordinate males were presented to the dominant male in nine meerkat groups during the oestrus period (4 – 12 days after parturition, Jordan et al. 2007) and the observable period of pregnancy (40 – 60 days after conception, Clutton-Brock et al. 2008) of the dominant female. As dominant females can have up to four breeding attempts during a single breeding season (Russell et al. 2003), it was possible to randomize the order of the presentations. These multiple breeding attempts also allowed us to subsequently validate the postpartum oestrus periods we designated, as all nine dominant females in the groups used were visibly pregnant within two months after the oestrus period presentations. Approximate conception dates for the seven pregnancies carried to term, estimated by backdating 70 days (gestation period in meerkats, Clutton-Brock et al. 2008) from the day that dominant females gave birth, fell within our oestrus windows. Faecal samples presented during the oestrus period of the dominant female did not differ in days since deposition from those presented during pregnancy (oestrus:  $\bar{x} = 4$  days, range 1 – 10; pregnant:  $\bar{x} = 5$  days, range 1 – 11; Wilcoxon signed-rank test:  $Z = -0.54$ ,  $P = 0.637$ ). We used samples from adult subordinate males that had prospected at the focal dominant male's group at least once during the current breeding season to control for familiarity.

### **6.3.6 Statistical analyses**

All statistical analyses were conducted using R (version 2.10.1; R Development Core Team 2011), with lme4 (version 0.999375-33; Bates et al. 2011) for fitting mixed models, coin (version 1.0-17; Hothorn et al. 2010) for Wilcoxon tests, and car (version 1.2-16; Fox 2009) for Box-Cox transformations. We analyzed data using Wilcoxon signed-rank tests when accounting for paired measures on the same individual, or Fisher's exact tests for count data when behaviours were rare. When

accounting for repeated measures of groups, we used general or generalized linear mixed models (LMM and GLMM) according to the distribution of the response variable. Initial mixed models included all potential explanatory variables and their interactions, which were then dropped in order of significance using a likelihood ratio test for model comparison, until minimal adequate models were achieved (Crawley 2007). Levels of significance and non-significance reported for explanatory terms were obtained by comparing minimal adequate models with models in which the term of interest had been added or removed. Post hoc comparisons were computed by dividing the differences between the parameter estimates from the minimal model by the standard error (SE) of the differences between them, and interpreting the output as a *t*-test using the residual degrees of freedom from the model (Zar 1999). A conservative approach was taken when calculating the residual degrees of freedom of a model, by using the difference between the number of observations and the maximum possible number of degrees of freedom associated with both random and fixed terms (Baayen et al. 2008).

To investigate the differences in responses to resident and foreign male faeces (experiment I), separate mixed models were used for each of the response variables, with faecal sample type (resident or foreign) and its two and three way interactions with sex and social status of the recipient individual included as explanatory variables. Age of the donor of the faecal sample varied between the two sample types (resident:  $\bar{x}$  = 531 days of age, range 291 – 1090; foreign:  $\bar{x}$  = 900 days of age, range 335 – 1374; Wilcoxon signed-rank test:  $Z = -4.23$ ,  $P < 0.001$ ) and was therefore fitted as a fixed effect in these models, along with order in which the sample was presented (first or second) and its interaction with sample type. One of our response variables, number of recruitment calls emitted, was zero-inflated and was therefore analyzed using two models. First, a binary model determined whether there were differences in the presence or absence of the response behaviour between presentations of resident and foreign samples and among categories of individual. We used a quasi-GLMM approach to account for the overdispersion detected in this first model with binomial error structure (Zuur et al. 2009). A second model included data only from individuals that emitted recruitment calls to at least one of the samples presented ( $n = 17$ ), to determine whether the differences from the number of recruitment calls emitted in

response to the foreign sample minus the number emitted in response to the resident sample, differed among categories.

## 6.4 Results

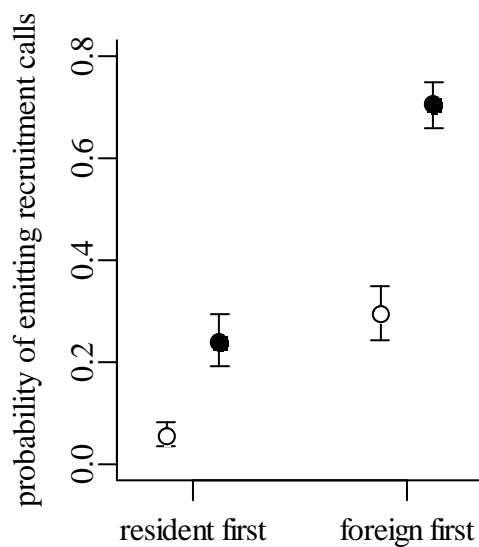
### 6.4.1 Sex and social status differences in responses to intruder scent marks

For all individuals tested, the likelihood of emitting recruitment calls was affected by an interaction between the sample type presented and the order of presentation, with the highest probability of emitting recruitment calls occurring when foreign faecal samples were presented first (table 6.1a). The greatest difference in probabilities of emitting recruitment calls between sample types occurred when the foreign sample was presented first (figure 6.1), but post hoc comparisons revealed that differences in probabilities were significant when it was presented second as well (foreign first  $t = 5.94$ , d.f. = 20,  $P < 0.001$ ; resident first  $t = 3.90$ , d.f. = 20,  $P < 0.001$ ). Dominant males showed the greatest difference in the number of recruitment calls emitted between presentations of resident and foreign samples, while dominant females showed the least (sex and social status interaction: table 6.1b; figure 6.2). Other group members approached the recipient individual in response to its recruitment calls on five occasions, in all of which a foreign faecal sample had been presented. The approaches occurred in response to the highest numbers of recruitment calls emitted (range 6 – 21), regardless of the identity of the caller. In terms of sample inspection time, there was a significant interaction between the type of sample presented and the sex of the recipient (table 6.1c, figure 6.3). Males, regardless of social status, spent significantly more time inspecting the foreign sample than the resident one, whereas females did not (LMM post hoc comparison: males  $t = 5.57$ , d.f. = 20,  $P < 0.001$ ; females  $t = 1.79$ , d.f. = 20,  $P > 0.05$ ). Males also inspected the foreign samples for longer than females (LMM post hoc comparison:  $t = 5.50$ , d.f. = 20,  $P < 0.001$ ). Dominant males were the only individuals who deposited counter-marks, and only did so when the sample presented was from a foreign male (5 out of 8 cases, compared to 0 for each of the other three categories of individual; Fisher's exact test:  $P = 0.001$ ).

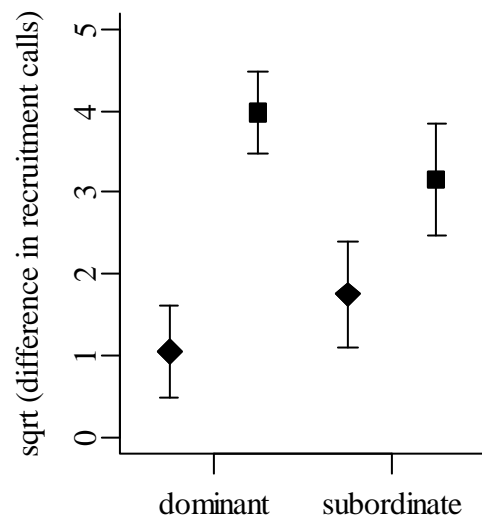


Dominant males used anal marks, urine, chewing and scuffing as counter-marks, which were placed near, but never directly on top (i.e., over-mark) of the foreign faecal sample ( $\bar{x} = 1.5$  counter-marks, range 0 – 5). There was no difference in the proportion of time individuals spent vigilant in the 10 minutes after presentations were conducted, between presentations of resident and foreign faecal samples (LMM: sample type:  $t = 1.15$ ,  $P = 0.256$ ).

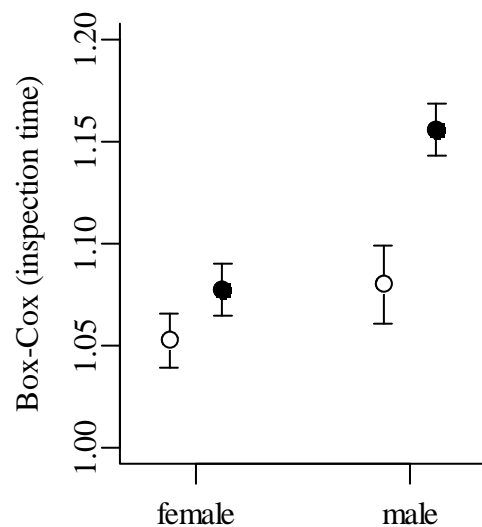
Males showed no difference in their responses to faeces of males from their own group, regardless of whether the sample presented had been collected while the donor was foraging with its group or prospecting. There were no differences between the sample types presented in the time spent inspecting the faeces ( $Z = 0.15$ ,  $P = 0.922$ ), number of recruitment calls emitted ( $Z = 1.01$ ,  $P = 0.312$ ) or proportion of samples counter-marked (one dominant male counter-marked both samples) by recipient males ( $n = 10$ ).



**Figure 6.1:** Effect of the interaction between sample type and order in which samples were presented on the probability that an individual ( $n = 31$ ) emitted at least one recruitment call during the presentation of a faecal sample (resident: open circle; foreign: filled circle). Circles show the mean of predicted values for females ( $n = 15$ ) and males ( $n = 16$ ) from the GLMM in table 6.1a ( $\pm 1$  SE, both converted to the original scale).



**Figure 6.2:** Effect of the interaction between sex and social status of the recipient on the difference in number of recruitment calls emitted between sample types presented (foreign – resident) for dominant and subordinate females (diamonds;  $n$  dominant = 3;  $n$  subordinate = 4) and males (squares;  $n$  dominant = 5;  $n$  subordinate = 5). Symbols show predicted values from the LMM in table 6.1b ( $\pm 1$  SE).



**Figure 6.3:** Effect of the interaction between sample type and sex of the recipient on the time females ( $n = 15$ ) and males ( $n = 16$ ) spent inspecting the faecal sample presented (resident: open circle; foreign: filled circle). Circles show predicted values from the LMM in table 6.1c ( $\pm 1$  SE).

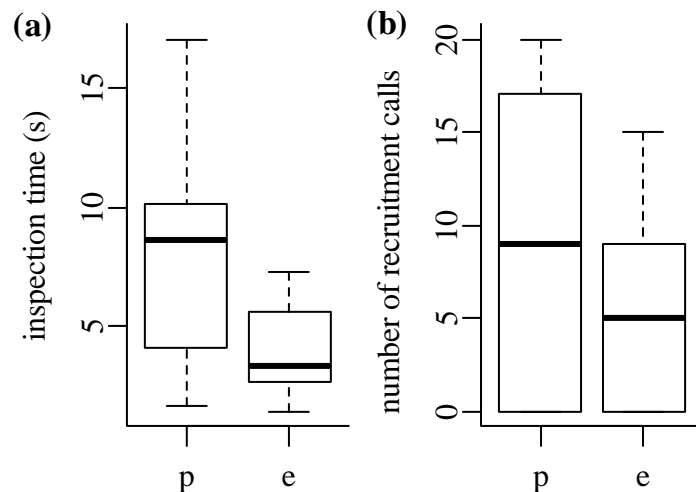
Response term	Explanatory terms	Estimate $\pm$ SE	<i>t</i>	<i>P</i>
(a) recruitment calls (yes, no)	(intercept)	-3.53 $\pm$ 0.42	-8.35	
	<b>sample type*order</b>	foreign*2 <sup>nd</sup> : -4.02 $\pm$ 0.53 (see figure 6.1)	-7.53	0.003
	<b>sample type</b>	foreign: +3.74 $\pm$ 0.44	8.49	
	<b>order</b>	2 <sup>nd</sup> : +1.99 $\pm$ 0.43	4.63	
	<b>sex</b>	male: +1.33 $\pm$ 0.24	5.48	0.040
	social status			0.999
	donor age			0.701
(b) difference in number of recruitment calls (square root)	(intercept)	+1.05 $\pm$ 0.57	1.84	
	<b>sex*social status</b>	male*sub.: -1.52 $\pm$ 0.71 (see figure 6.2)	-2.13	0.027
	<b>sex</b>	male: +2.92 $\pm$ 0.64	4.55	
	<b>social status</b>	subordinate: +0.70 $\pm$ 0.56	1.25	
	<b>donor age diff.</b>	-0.00 $\pm$ 0.00	-2.01	0.030
	order			0.661
(c) time spent inspecting sample (Box-Cox transformed)	(intercept)	+1.05 $\pm$ 0.01	80.91	
	<b>sample type*sex</b>	foreign*male: +0.05 $\pm$ 0.02 (see figure 6.3)	2.58	0.010
	<b>sample type</b>	foreign: +0.03 $\pm$ 0.01	1.79	
	<b>sex</b>	male: +0.03 $\pm$ 0.01	1.94	
	<b>order</b>	2 <sup>nd</sup> : -0.03 $\pm$ 0.01	-2.70	0.007
	social status			0.605
	donor age			0.895

**Table 6.1:** Factors influencing an individual's (a) probability of emitting recruitment calls, (b) difference in number of recruitment calls emitted (foreign – resident), and (c) time spent inspecting samples, during presentations of faecal samples. Shown are the results of LMMs and a GLMM fitted with group identity as a random term. Individual identity was also fitted as a random term in (a) and (c). Quasi-binomial errors were used for (a). Explanatory terms and interactions highlighted in bold were included in the minimal models.

#### 6.4.2 Temporal variation in response to intruder scent marks by dominant males

Dominant males spent less time inspecting the foreign samples presented when the resident dominant female was in oestrus than when pregnant ( $Z = 2.31$ ,  $P = 0.020$ ; figure 6.4a), but there was no difference in number of recruitment calls emitted ( $Z =$

0.84,  $P = 0.453$ ; figure 6.4b). Dominant males only counter-marked the sample presented when the dominant female was pregnant ( $\bar{x} = 1.4$  counter-marks, range 0 – 7), but the proportion of individuals that counter-marked (4 out of 9) was not significantly different from zero (Fisher's exact test:  $P = 0.082$ ). There were no significant differences between the two reproductive phases in the proportion of time dominant males spent vigilant ( $Z = 1.48$ ,  $P = 0.164$ ) or mate-guarding ( $Z = -0.95$ ,  $P = 0.391$ ) after the presentations. When comparing only among control focal observations for each behaviour, there were no differences between pregnant and oestrus period observations (vigilance:  $Z = -0.77$ ,  $P = 0.496$ ; mate-guarding:  $Z = 1.54$ ,  $P = 0.148$ ).



**Figure 6.4:** Influence of the resident dominant female's reproductive status (p: pregnant; e: oestrus) on (a) the time spent inspecting the faecal samples and (b) the number of recruitment calls emitted by dominant males ( $n = 9$ ) during presentations. Boxplots show the median (line within boxes), 25 and 75% quartiles (lower and upper ends of boxes) and 1.5 times the inter-quartile range (dashed lines) of the data.

## 6.5 Discussion

Meerkats showed distinct responses to faeces from extra-group males compared to those from resident males, in accordance with empirical and experimental studies on scent mark discrimination in other group-living carnivores (e.g., European badger:

Buesching et al. 2002; banded mongoose: Müller and Manser 2007; spotted hyena: Burgener et al. 2008). Dominant males had the strongest response to intruding male scent marks, consistent with the idea that intense reproductive conflict with extra-group individuals predicts strong responses to intruders of the same sex. The increased alarm behaviour to intruder scent marks across all categories of individual suggests that other group members may also participate in repelling intruders, for reasons other than mate defence. Although sex (Gosling and Roberts 2001; Palagi and Dapporto 2007) and social status (Thiessen and Rice 1976; Hurst 1990) are known to affect responses to intruder scent marks, our results are the first to show detailed differences in individual responses to intruder scent marks in a cooperative breeder with high reproductive skew.

Individuals of all sex and social status combinations were more likely to emit recruitment calls when presented with faeces from intruders than with resident male faeces, supporting previous observations that meerkats respond to encounters with foreign scent marks by emitting recruitment calls (Manser 2001). We interpret these calls as a correlate of response intensity to a perceived threat, as similar alarm-like vocalizations are emitted by meerkats when encountering secondary cues from predators (Manser 2001) and are also used by banded mongooses in similar contexts (Cant et al. 2002; Müller and Manser 2008). This general response may seem to conflict with the idea that the defence of breeding opportunities is the primary reason for strong responses to intruders. However, as well as affecting the reproductive success of dominant males, extra-group males may increase the reproductive conflict between dominant and subordinate females (Clutton-Brock et al. 2001b; Griffin et al. 2003), and can reduce the inclusive fitness of all resident subordinates by reducing their relatedness to the young they help rear. Alternatively, all individuals may be alarming initially to the presence of a foreign scent, without knowing if the intruder is a single individual or a whole group. Intruding groups can be a serious threat to all resident individuals, through the potential loss of territory and, when pups are present in the group (in all but six of the presentations in experiment I), through infanticide (Young 2003). As meerkats respond to recruitment calls by joining the caller (Manser 2001), alarming at intruder scent marks may ultimately distribute the costs of defending a group's resources.

Unlike dominant and subordinate females, all male meerkats spent significantly more time inspecting the foreign faecal samples than the resident male samples. This is in contrast to the absence of sex-specific responses to intruder scents suggested in badgers (Palphramand and White 2007), a species where extra-group mating is also common (Dugdale et al. 2007). Palagi and Dapporto (2007) suggested that dimorphism in responses to scent cues reflects differences in motivation and territorial defence, which should be influenced by the perceived level of threat that an intruder poses to a resident individual. Intruding males in big enough coalitions relative to the number of resident males may take over established breeding groups, expelling all males in the process (Young 2003). Resident males are thus expected to respond more aggressively to same-sex intruders, as has been suggested in meerkats (Doolan and Macdonald 1996b; Young et al. 2005) and in many other mammal species (e.g., lion: Heinsohn et al. 1996; spotted hyena: Boydston et al. 2001; common marmoset: Lazaro-Perea 2001; banded mongoose: Cant et al. 2002). Detecting and identifying extra-group males through their scent marks could allow resident males to quickly identify intruders later on through scent matching (Gosling 1982; Hurst and Beynon 2004). This may benefit resident males by eliminating the need to inspect the intruders themselves, thus reducing the time needed to respond to intruder approaches appropriately.

The strongest response to intruding male scent marks was observed in dominant males, who showed the highest increase in number of recruitment calls emitted and were the only ones to counter-mark when presented with the foreign faecal samples. Dominant individuals in other social species also counter-mark same-sex intruder scent marks more frequently than subordinates (Thiessen and Rice 1976; Hurst 1990), potentially as a reaffirmation of competitive ability and commitment to defend resources (Hurst and Beynon 2004). Our results are in sharp contrast with those reported for banded mongooses, however, where all resident males counter-mark scent marks deposited by male group members, reflecting the high within-group reproductive conflict (Müller and Manser 2008). A previous study on meerkat latrine behaviour found that dominant and subordinate males deposit scent marks and over-mark female scent marks from their own group at similar rates, potentially as a form of both territory and mate defence (Jordan 2007). We suggest that the absence of

counter-marking (and over-marking) by subordinate males and the preferential counter-marking of foreign over resident faeces by dominant males in our study, support the idea that mate defence may be the primary motivation for counter-marking intruding male scent marks.

Given that males may be adjusting their responses to other males according to levels of reproductive conflict, it is perhaps surprising that dominant males did not increase the intensity of their response to intruder faeces when dominant females were most receptive. On the contrary, dominant males significantly reduced the time they invested inspecting faecal samples and never counter-marked the faecal sample presented when the resident dominant female was in oestrus. Kutsukake and Clutton-Brock (2008) argued that intense mate-guarding during the oestrus period of the dominant female imposed time and energy constraints on dominant males, which could explain our results. However, we did not find any differences in the time dominant males spent mate-guarding during pre-presentation (control) focal observations, between the two reproductive phases of the dominant female. It is possible that dominant males are in fact mate-guarding, hence the reduction in time spent inspecting the samples during oestrus, but our measure of mate-guarding may have been too restrictive. As meerkats are active during the day and typically forage in open areas, effective mate-guarding may not require that a dominant male remain in close proximity to the dominant female. The absence of an increase in, or the complete lack of counter-marking by dominant males during the dominant female oestrus period in our study, could be due to limitations on scent mark production (e.g., faeces: Brashares and Arcese 1999; urine: Hurst and Beynon 2004) and to shifts in male scent-marking priorities. Within meerkat groups, males selectively over-mark female scent marks, which has been suggested as a way of masking the presence of females from extra-group males (Jordan 2007). If as in other species (e.g., Alaskan moose: Bowyer et al. 1994; meadow vole: Ferkin et al. 2004; ringtailed lemur: Scordato and Drea 2007), female meerkats increase their rates of scent-marking during oestrus, dominant males may be under increased demand to over-mark female scent marks, which could impede any increase in counter-marking rates of intruder faeces. Further research on female scent-marking behaviour and its potential effect on male counter-marking patterns are warranted.

In conclusion, we found experimental evidence that meerkats of all sex and social status respond differently to intruding male than to resident male faeces. In accordance with the sex-specific responses to intruders observed in other species, we also showed that resident males spent more time inspecting intruder faeces than resident faeces, but females did not. Moreover, among males, social status was important in determining the response intensity towards intruding male faeces. We found that dominant males had the strongest overall response to intruding male faeces, as predicted by the potentially high level of reproductive conflict between resident dominant and subordinate extra-group males, but investment in some of these response behaviours may in fact decrease when females are most receptive. Although we did not test resident individuals' responses to scent marks of all types of territorial intruders (e.g., prospecting male coalitions, foreign groups), our results suggest that, in cooperatively breeding species, all members of a group may participate in resource defence, but sex and social status may affect an individual's investment in deterring male intruders.



## CHAPTER 7

# General Discussion

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### 7.1 Overview

In cooperatively breeding species, where dominant individuals are the primary breeders, subordinates help raise young and largely forego their own reproduction until they acquire a dominant position in the natal group or disperse. If the primary limiting factors preventing subordinates from breeding in their natal group are a lack of unrelated partners and strong inbreeding avoidance, individuals may conduct extraterritorial prospecting forays both to assess dispersal opportunities and to access mating opportunities in neighbouring groups. As a result, prospectors can affect the fitness of individuals residing in the groups they approach, but the effects of their intrusions are likely to differ greatly among resident individuals given that most cooperative groups experience high levels of reproductive competition.

In this dissertation, I investigated two broad questions relating to prospecting in cooperative breeders: (i) what are the causes and consequences of individual variation in investment in prospecting behaviour by subordinate males, and (ii) what are the causes and consequences of individual variation in responses to prospectors by resident individuals? In this chapter, I discuss my findings and offer suggestions for future work.

## **7.2 Causes and consequences of variation in prospecting behaviour**

### **7.2.1 Subordinate males prospect when the benefits are high and costs low**

Prospecting allows individuals to acquire information on future dispersal options (Waser 1996; Reed et al. 1999; Danchin et al. 2001) and also to access extra-group breeding opportunities (Westneat and Stewart 2003). Extraterritorial forays are costly (e.g., increased risk of predation), however, so individuals may differ in their investment in prospecting depending on the relative costs incurred and may time their forays according to the availability of dispersal or mating opportunities.

In Chapter 3, I showed that prospecting by subordinate male meerkats follows a consistent seasonal pattern which broadly coincides with periods when both female fertility and numbers of evicted females across the population are high, and when rainfall is low. I did not find, however, any strong, independent effects of population- or group-level oestrus and eviction patterns, or of rainfall (which could predict both fertility and eviction patterns across the population), on the timing of prospecting forays, suggesting that these events themselves may not act as the stimuli for the observed seasonal patterns. Nonetheless, investment in prospecting by subordinate males is highest when there appear to be more opportunities for dispersal than average in a given period (i.e., a high number of evicted females in the population). One possible explanation for this finding is that males increase their investment in prospecting if they encounter evicted females on a foray, although detailed data on such events were not available from the long-term dataset and would require following prospecting males and evicted females in the field. More generally, there is scope for future work to understand the seasonal cues which predict individual decisions to leave the natal group.

In addition to broad seasonal patterns, proximity between groups plays an important role in the timing of prospecting forays, as indicated by the observed positive correlation between intergroup encounters and the probability of prospecting (Chapters 3 and 4). Given the importance of direct encounters with neighbouring groups, secondary cues (e.g., scent marks) of neighbouring groups may be significant for the timing of prospecting forays. Meerkats are able to discriminate between their own group and extra-group scents (Chapter 6), and olfactory cues presumably convey additional information on an individual's identity, sex, health and reproductive status (Hurst and Beynon 2004). Indeed, previous studies have found that prospecting meerkats actively investigate scent marks from neighbouring groups and suggest that these secondary cues could provide information on group composition and female reproductive status (Doolan and Macdonald 1996b; Jordan et al. 2007). Furthermore, in banded mongooses, males have been observed leading their group into encounters with another group shortly after investigating the scent cues of a neighbouring group (Cant et al. 2002). Encounters with scent cues could, therefore, suggest the proximity of a neighbouring group and convey additional information regarding mating and dispersal opportunities for prospecting males. Further work on the role of secondary cues, and the information contained therein, for the timing of prospecting forays is warranted.

Numerous studies have shown the costs and risks associated with extraterritorial forays (e.g., Lazaro-Perea 2001; Young et al. 2005; Young and Monfort 2009; Raihani et al. 2010; Chapter 5) and the results presented in Chapters 3 and 4 suggest that individuals modulate their investment in prospecting so as to mitigate such costs. Individuals that are heavier, for example, are likely to be better able to cope with the costs of prospecting than lighter individuals, as has been suggested for dispersal (Dufty and Belthoff 2001). Accordingly, I found that males who are heavier for their age are more likely to prospect than lighter males. This potential advantage in condition does not appear to allow males to extend the duration of their prospecting forays, however, as I found that body mass does not affect whether or not males returned on the same day as departing on an extraterritorial foray (Chapter 3). Males, regardless of age or body mass, typically return to their groups on the same day as departing on a foray, and are more likely to do so when their own group is babysitting or is involved in an intergroup interaction. These

results suggest that the duration of forays may be influenced by the distance prospectors have to travel between groups and the ease with which prospectors may be able to find their own group when attempting to return from a foray, rather than on any strategic modulation. Whereas males may be able to modulate the frequency with which they prospect according to their age and condition, the costs associated with extending the amount of time they spend away from their groups while on forays may be prohibitively high.

Together, the benefits and costs of prospecting are likely to determine the timing of extraterritorial forays and the extent to which subordinate males invest in prospecting. Investigating the benefits and costs of prospecting are likely to shed light not only on the patterns of extraterritorial prospecting, but also on patterns of subordinate reproduction and dispersal (e.g., Double and Cockburn 2003; Young et al. 2007; Clutton-Brock et al. 2008). Furthermore, as investment in prospecting may also have effects on the amount of helping subordinates are able or willing to contribute (Young et al. 2005; Chapter 4), individual variation in investment in prospecting should be taken into account in broader studies on cooperative behaviour and in particular, on the evolution of cooperative breeding.

### **7.2.2 Subordinate males that can invest more in prospecting help less**

In cooperative breeders, individuals typically vary in their contributions to helping behaviours (Komdeur 2006; Bergmüller et al. 2010) and recent evidence suggests that these differences may be consistent throughout individuals' lives (English et al. 2010). Consistent behavioural differences between individuals may arise from formative processes during early life (Biro and Stamps 2008) that may ultimately lead to trade-offs between breeding and helping behaviours (Cant and Field 2001) later in life.

In Chapter 4, I found that early-life body mass had divergent effects on investment in prospecting and contributions to helping later in life in subordinate males. Males that were heavier at the age of nutritional independence (approximately three months old) started prospecting at an earlier age and subsequently contributed less to feeding dependent young within their first 18 months of life than lighter males. Although trade-offs between current prospecting effort and pup feeding have previously been shown in adult male meerkats (Young et al. 2005), my results suggest

that the propensity to help may be determined during early development: first, recent prospecting effort was controlled for in my analyses and had no effect on a male's contributions to helping, and, second, helping data was not collected within a week of a prospecting foray. That heavier males at nutritional independence did not subsequently contribute more to feeding pups than lighter males, regardless of recent prospecting effort, is perhaps surprising, given that helping is costly and individuals that are heavier are typically able to help more (Heinsohn and Legge 1999; Clutton-Brock et al. 2002). These results, however, lend support to predictions from theoretical models that individuals should reduce their contributions to helping when their future chances of breeding independently are high (Cant and Field 2001).

A mechanism by which early-life body mass may have downstream effects on investment in prospecting and helping is through its effect on body mass later in life. Indeed, I found that body mass at nutritional independence was positively correlated with body mass at 6 and 12 months of age (Chapter 4). Furthermore, body mass later in life (adjusted for age) explained more variance in the age of onset of prospecting than early-life body mass. Heavier males, therefore, may be better able to cope with the costs of prospecting than lighter males throughout their lives (Chapters 3 and 4). In contrast to the effect of body mass later in life on investment in prospecting, I found that a male's early-life body mass explained more variance in his subsequent contributions to pup feeding than his body mass at the time the behaviours were measured later in life (Chapter 4). This result suggests that male meerkats' propensity to contribute to cooperative care may be set from an early age and relatively fixed throughout their lives, as has been suggested to occur with a number of behavioural traits in other animals (e.g., aggression and sociality; reviewed in Sih et al. 2004). A recent review by Soares et al. (2010) suggests that differences in hormonal profiles during development may have subsequent effects on cooperative behaviours, and these hormonal differences could well be correlated with differences in body mass (e.g., Duckworth et al. 2001; Liang and Zhang 2006). Future work could examine the role of specific hormones, such as cortisol, in mediating these consistent individual differences.

Ultimately, males may be pursuing alternative life-history tactics that best suit their state (McNamara and Houston 1996), based on the relative fitness payoffs from investing in prospecting and helping. My study contributes to a growing appreciation

that investigating the trade-offs between different behaviours, rather than focusing on the factors underlying one particular trait at a given time point, may help elucidate longer-term life-history trajectories (e.g., Schürch and Heg 2010). Moreover, conditions in early-life can play a crucial role in setting individuals on these trajectories (Stamps 2007; Biro and Stamps 2008). Cooperative species provide an interesting model in which to understand these links, given that subordinate individuals often face a stark trade-off between investing in breeding or helping (at any given time) (e.g., Young et al. 2005), or between investing in helping now versus saving resources for reproduction later (Cant and Field 2001).

My results in Chapter 3 and 4 both indicate an influence of body mass on investment in prospecting by subordinate males. Taken together, these results highlight the importance of helpers on future reproductive success among subordinate males, given the previously shown effect of helper contributions to care on an individual's body mass at nutritional independence (e.g., Hatchwell et al. 2004; Ridley 2007; Russell et al. 2007). Interestingly, individuals that receive the benefits of increased cooperative care during early development appear to subsequently reduce their contributions to care (English 2009; Chapter 4) which could have strong implications for the maintenance of cooperative behaviours if subsequent generations receive less care. Alternatively, as individuals that are in better condition early in life are typically born to larger groups (e.g., Clutton-Brock et al. 2001c) and subsequently become helpers in these larger groups, any individual reductions in contributions to care may be offset by the increased number of helpers.

## **7.3 Causes and consequences of variation in responses to prospectors**

### **7.3.1 Residents invest in repelling prospectors according to the benefits and costs**

In group-living species, individuals may differ markedly in their contributions to repelling territorial intruders that are typically in search of breeding or dispersal opportunities (Møller 1987). Differential benefits and the relative costs of repelling these intruders are likely to play key roles in mediating individual differences in contributions to territory defence, particularly in species with high reproductive skew (Nunn 2000).

In Chapter 5, I showed that both dominant and subordinate males invest more in chasing prospectors than females and that this sex difference in contributions to defence can be explained by the benefits of repelling intruders. Males benefit more from repelling prospectors than females, as males may lose dominance and be expelled during intrusions whereas females do not face these risks. Sex-specific responses to intruders are widespread, with residents typically responding most aggressively towards intruders of the same sex owing to potential reproductive conflict (Møller 1987; Boydston et al. 2001; Cant et al. 2002). In group-living species with dominance hierarchies, therefore, dominant males may be expected to invest more than subordinate males in repelling male intruders, particularly when breeding opportunities for subordinates are limited within the group (e.g., Cooney 2002). Nonetheless, I found that both dominant and older subordinate males invested equally in chasing prospectors, in a seemingly cooperative form of territory defence, though males were responding to different benefits of repelling intruders and preventing extra-group copulations: dominants may accrue direct fitness benefits, whereas subordinates gain indirect benefits from helping to raise offspring fathered by the dominant male (typically their own father; Griffin et al. 2003; Spong et al. 2008), rather than by extra-group males. Alternatively, both dominant and subordinate males may be responding to the threat of being expelled from the safety of their group.

Although the different benefits of territory defence among resident males did not lead to differences in investment in repelling intruders, I found that males did modulate how much they chased intruders in accordance with the costs. Males, who invest heavily in territorial defence, experience a cost in the form of reduced weight gain when prospectors are present, whereas resident females, who do not chase prospectors, show no such reductions in weight gain in the presence of prospectors (Chapter 5). Indeed, chasing intruding individuals has also been shown to be energetically costly in other species (e.g., stitchbirds: Low 2006). As a result of this cost of repelling prospectors, males that are heavier for their age invest more in leading chases of prospectors than lighter males. These results suggest that although body mass may not be important for the acquisition of dominance in male meerkats (Spong et al. 2008), it may play a significant role in preventing extra-group copulations and have important fitness consequences for both dominant and subordinate males.

I also found evidence of a second cost associated with the presence of prospectors, which was not restricted solely to those individuals engaged in chasing. Both male and female residents reduced their contributions to feeding dependent young when a prospector was present at their group, resulting in reduced overall rates of weight gain among pups. Accordingly, males reduced the rate at which they led chases of prospectors when their groups contained dependent young. Among males, this pattern of lower feeding rates in the presence of prospectors could reflect an energetic trade-off between chasing and pup feeding, as contributions to pup feeding are state-dependent (Clutton-Brock et al. 2001a; Clutton-Brock et al. 2002). A similar explanation for the reduction in feeding rates by females is unlikely, however, as females chased substantially less than males and did not suffer reductions in weight gain. One possibility is that the presence of prospectors and the chasing ensued may disrupt normal foraging and care activities even for residents that do not take an active role in repelling prospectors. Females, particularly those with greater chances of breeding, may prioritise maintaining their own condition rather than feeding pups under these circumstances. Indeed, dominant and older females reduced their contributions to feeding, whereas reproductively immature females increased their contributions in the presence of prospectors. To my knowledge, this is one of the first studies to demonstrate that the presence of prospectors may have a diffuse effect on all individuals in the group, even if they do not actively chase prospectors.

Taken together, these findings regarding individual differences in contributions to prospector repulsion highlight the importance of considering both the benefits and costs associated with the investment in cooperative activities such as territory defence when investigating individual variation in contributions (Nunn 2000). When the potential costs of repelling intruding individuals are extremely high, striking differences in contributions may arise between resident individuals (e.g., Grinnell et al. 1995; Heinsohn and Packer 1995). In meerkats, given the relatively low costs of chasing prospectors in comparison to the benefits gained by all resident males, dominant and subordinate males appear to contribute equally to repelling prospectors.



### **7.3.2 Responses to prospector scent cues are affected by sex and social status**

In the context of territorial interactions, scent marking is expected to allow residents to advertise territory ownership and their competitive abilities (Gosling 1982; Wyatt 2003; Hurst and Beynon 2004). In species where individuals conduct extraterritorial prospecting forays in search of mating and dispersal opportunities, scent marking may also allow individuals to advertise their presence to potential mates and challenge territory owners (Gosling and Roberts 2001; Hurst and Beynon 2004).

In Chapter 6, I showed that meerkats are able to discriminate between scent marks of extra-group males and scent marks from males within their own groups. All residents were more likely to emit alarm calls when investigating the scent of an extra-group male than the scent of a resident male. Males also investigated extra-group male scent marks for longer than resident male scent marks, whereas females did not. This sex difference in responses to scent marks could reflect differences in an individual's motivation to investigate scent marks and in the level of threat that an intruder poses to a resident individual (Palagi and Dapporto 2007). Accordingly, as resident males are at risk of being expelled from their groups by prospectors and females are not (Chapter 5), males spent more time investigating extra-group male scent marks than females (Chapter 6). By investigating the scent marks of intruding males for longer than females, males may become familiar with intruder scents and be able to quickly identify them later on through scent matching (Gosling 1982; Hurst and Beynon 2004). As resident males invest substantially in chasing prospecting males (Chapter 5), identifying extra-group males correctly through their scent may be a valuable first step in keeping intruders at bay.

While dominant and subordinate males invested similarly in chasing prospectors (Chapter 5), they differed markedly in their responses to intruder scent marks (Chapter 6). Only dominant males counter-marked extra-group male scent marks, suggesting a direct role of counter-marking in mate defence, rather than broader territory defence. A similar use of counter-marking has been observed in the banded mongoose, where resident males compete with each other for breeding opportunities within the group and selectively counter-mark scent marks deposited by other male group members (Müller and Manser 2008). I did not find, however, an increase in counter-marking by dominant males when dominant females were in oestrus, compared to when they were not (Chapter 6), possibly due to the

physiological limitations of scent mark production (Brashares and Arcese 1999; Hurst and Beynon 2004). Nonetheless, these results suggest that although both dominant and subordinate males benefit from repelling prospectors and contribute equally to chasing them (Chapter 5), state-dependent tactics may have evolved according to the specific benefits of repelling intruders for resident males.

## **7.4 Future work**

Due to the logistical limitations of tracking prospecting individuals, I have not attempted to distinguish between the two main benefits that prospecting males may accrue during extraterritorial forays: attempting to mate with females that are resident in neighbouring groups and assessing dispersal opportunities with evicted females. Mating is cryptic in meerkats, with individuals typically moving away from their groups before copulating. Similarly, both prospectors and evicted females (with whom prospectors are known to associate) can move outside of the usual range of the study groups, making it particularly difficult to follow them. Recent technological developments may allow future studies to address the specific question of how much time prospectors spend at neighbouring groups versus associating with evicted females. Collars fitted with global positioning system (GPS) tracking units and proximity loggers have recently become more widely used in studies of animal movement (Prange et al. 2006; Tomkiewicz et al. ) and could shed additional light on whether prospectors are primarily in search of mating or dispersal opportunities. The use of GPS collars could provide more detailed information on the precise costs of extraterritorial movements, in terms of distance travelled, search time and duration of forays, as well as provide interesting insights into how new groups are formed.

A fruitful future avenue of exploration could involve combining genetic measures of paternity in meerkats with data on individual variation in investment in prospecting. Although a previous study investigated the correlation between investment in prospecting and subordinate male extra-group reproductive success (Young et al. 2007), a broad study on the potential importance of body mass and condition for male reproductive success has yet to be done. Body mass does not seem to play a role in determining dominant male reproductive success (Spong et al. 2008), yet it may be important for subordinate males, as suggested by the positive correlation

found between body mass and investment in prospecting in this dissertation. Furthermore, combining paternity and prospecting data could shed additional light on the effect of early-life conditions on future fitness in males.

## **7.5 Conclusions**

Prospecting behaviour is likely to influence dispersal decisions, patterns of within and extra-group reproduction and contributions to helping, yet little attention has been paid to the extent to which investment in prospecting may vary across individuals. In this dissertation, I examined the factors that affect individual variation in investment in prospecting behaviour by males, from its early development to the patterns observed later in life, and how this investment may affect a male's contributions to helping. Similarly, I investigated how contributions to territorial defence and responses to secondary cues of prospectors varied between resident individuals according to the benefits and costs of repelling prospectors. Prospecting presents a route to current and future fitness for subordinates in cooperative societies, as well as contrasting fitness consequences to resident individuals, depending on whether they gain or lose reproductive opportunities on encountering a foreign individual. As such, understanding individual variation in investment in prospecting and in responses to prospectors may provide a relatively novel insight into our understanding of the maintenance and evolution of cooperative breeding and cooperation in general.



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**APPENDIX I****Species common and scientific names**

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**Kingdom Animalia****Class Mammalia****Order Carnivora**

African wild cat	<i>Felis silvestris lybica</i>
Banded mongoose	<i>Mungos mungo</i>
Cape fox	<i>Vulpes chama</i>
Caracal	<i>Caracal caracal</i>
Dwarf mongoose	<i>Helogale parvula</i>
European badger	<i>Meles meles</i>
Lion	<i>Panthera leo</i>
Meerkat	<i>Suricata suricatta</i>
Spotted hyena	<i>Crocuta crocuta</i>

**Order Cetartiodactyla**

Alaskan moose	<i>Alces alces gigas</i>
Blue wildebeest	<i>Connochaetes taurinus</i>
Common eland	<i>Taurotragus oryx</i>
Gemsbok	<i>Oryx gazella</i>
Red hartebeest	<i>Alcelaphus caama</i>
Springbok	<i>Antidorcas marsupialis</i>

**Order Primates**

Chimpanzee	<i>Pan troglodytes</i>
Common marmoset	<i>Callithrix jacchus</i>
Golden lion tamarin	<i>Leontopithecus rosalia</i>
Ringtailed lemur	<i>Lemur catta</i>
Ursine colobus monkey	<i>Colobus vellerosus</i>

**Order Rodentia**

Belding's ground squirrel	<i>Spermophilus beldingi</i>
Damaraland mole-rat	<i>Cryptomys damarensis</i>
House mouse	<i>Mus domesticus</i>
Meadow vole	<i>Microtus pennsylvanicus</i>
Naked mole-rat	<i>Heterocephalus glaber</i>

**Class Aves****Order Coraciiformes**

Micronesian kingfisher	<i>Todiramphus cinnamominus reichenbachii</i>
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**Order Falconiformes**

Black-breasted snake eagle	<i>Circaetus pectoralis</i>
Gabar goshawk	<i>Melierax gabar</i>
Lanner falcon	<i>Falco biarmicus</i>
Martial eagle	<i>Polemaetus bellicosus</i>
Pale chanting goshawk	<i>Melierax canorus</i>
Steppe buzzard	<i>Buteo buteo vulpinus</i>
Tawny eagle	<i>Aquila rapax</i>

**Order Passeriformes**

Stitchbird	<i>Notiomystis cincta</i>
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**Order Phoenicopteriformes**

Greater flamingo	<i>Phoenicopeterus ruber roseus</i>
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**Class Reptilia****Order Squamata**

Cape cobra	<i>Naja nivea</i>
Puff adder	<i>Bitis arietans</i>

## **Kingdom Plantae**

### **Class Magnoliopsida**

#### **Order Capparales**

Shepherd's tree

*Boscia albitrunca*

#### **Order Fabales**

Blackthorn

*Acacia mellifera*

Camelthorn

*Acacia erioloba*

#### **Order Lamiales**

Drie doring

*Rhigozum trichotomum*

#### **Order Malvales**

Raisin bush

*Grewia flava*

#### **Order Poales**

Sour grass

*Schmidtia kalahariensis*

## APPENDIX II

## Candidate model sets for analyses in Chapter 5

Candidate models for each of our analyses (see methods in Chapter 5). For each table: AICc = Akaike's information criterion value corrected for small sample sizes; d.f. = number of estimated parameters;  $\Delta_i$  = the model's AICc minus the minimum AICc among candidate models;  $\log(L)$  = log-likelihood. For each candidate set of models: AC = age category; ASC = age and social status category; GS = group size; M = age-corrected body mass; Pros = prospector present or absent; nPros = number of prospectors; Pups = pups foraging with the group or not; aPup = modal pup age; nPups = number of pups foraging with the group; R = total rainfall in past month; SS = social status.

**Table A2.1:** Proportion of chases led per observation session

Fixed terms	$\log(L)$	d.f.	AICc	$\Delta_i$
Sex	-94.95	3	196.10	0.00
Sex * Pups	-93.51	5	197.54	1.44
Sex + Pups	-94.91	4	198.15	2.06
Sex * Pups + GS + nPros	-91.84	7	198.64	2.55
Sex + Pups + GS + nPros	-93.21	6	199.14	3.05
Sex * Pups + GS * nPros	-91.59	8	200.43	4.34
Sex + Pups + GS * nPros	-92.95	7	200.87	4.78
Intercept only	-225.95	2	456.00	259.90

**Table A2.2:** Rate of chases led by males (leads/h)

Fixed terms	$\log(L)$	d.f.	AICc	$\Delta_i$
AC + M + GS * nPros + Pups	-395.82	11	814.32	0.00
ASC + M + GS * nPros + Pups	-395.72	12	816.23	1.91
AC + GS * nPros + Pups	-398.43	10	817.43	3.10
ASC + GS * nPros + Pups	-398.43	11	819.54	5.22
SS + M + GS * nPros + Pups	-403.33	10	827.22	12.90
GS * nPros + Pups	-406.32	8	829.01	14.69
SS + GS * nPros + Pups	-405.70	9	829.86	15.53



**Table A2.3:** Rate of weight gain (g/h)

Model set	Fixed terms	log(L)	d.f.	AICc	$\Delta_i$
(a) Males	ASC * Pros + R + R <sup>2</sup>	-5935.11	15	11900.44	0.00
	ASC * Pros + M + R + R <sup>2</sup>	-5935.63	16	11903.50	3.07
	AC * Pros + R + R <sup>2</sup>	-5944.86	13	11915.89	15.46
	AC * Pros + M + R + R <sup>2</sup>	-5945.39	14	11918.96	18.53
	SS * Pros + R + R <sup>2</sup>	-5953.83	9	11925.73	25.30
	SS * Pros + M + R + R <sup>2</sup>	-5953.12	10	11926.33	25.90
	ASC + Pros + R + R <sup>2</sup>	-5956.32	11	11934.75	34.32
	ASC + M + Pros + R + R <sup>2</sup>	-5956.78	12	11937.70	37.26
	ASC + R + R <sup>2</sup>	-5958.91	10	11937.93	37.49
	AC + Pros + R + R <sup>2</sup>	-5959.65	10	11939.40	38.96
	ASC + M + R + R <sup>2</sup>	-5959.38	11	11940.89	40.45
	AC + M + Pros + R + R <sup>2</sup>	-5960.16	11	11942.45	42.01
	AC + R + R <sup>2</sup>	-5962.29	9	11942.67	42.23
	AC + M + R + R <sup>2</sup>	-5962.81	10	11945.72	45.28
	Pros + R + R <sup>2</sup>	-5970.53	7	11955.11	54.67
	SS + M + Pros + R + R <sup>2</sup>	-5968.90	9	11955.89	55.46
	SS + Pros + R + R <sup>2</sup>	-5969.98	8	11956.02	55.59
	R + R <sup>2</sup>	-5973.40	6	11958.84	58.40
	SS + M + R + R <sup>2</sup>	-5971.75	8	11959.57	59.14
	SS + R + R <sup>2</sup>	-5972.83	7	11959.72	59.28
(b) Females	AC + R + R <sup>2</sup>	-4602.82	9	9223.74	0.00
	ASC + R + R <sup>2</sup>	-4602.53	10	9225.19	1.45
	AC + Pros + R + R <sup>2</sup>	-4602.87	10	9225.87	2.13
	AC * Pros + M + R + R <sup>2</sup>	-4598.83	14	9225.90	2.16
	AC + M + R + R <sup>2</sup>	-4603.14	10	9226.40	2.66
	ASC + Pros + R + R <sup>2</sup>	-4602.58	11	9227.32	3.58
	ASC + M + R + R <sup>2</sup>	-4602.85	11	9227.85	4.11
	AC + M + Pros + R + R <sup>2</sup>	-4603.19	11	9228.52	4.78
	ASC * Pros + R + R <sup>2</sup>	-4599.69	15	9229.65	5.91
	AC * Pros + R + R <sup>2</sup>	-4601.87	13	9229.94	6.20
	ASC + M + Pros + R + R <sup>2</sup>	-4602.90	12	9229.98	6.23
	ASC * Pros + M + R + R <sup>2</sup>	-4600.03	16	9232.38	8.63
	SS + R + R <sup>2</sup>	-4620.38	7	9254.82	31.08
	SS * Pros + R + R <sup>2</sup>	-4618.56	9	9255.22	31.48
	SS + M + R + R <sup>2</sup>	-4619.58	8	9255.24	31.50
	SS * Pros + M + R + R <sup>2</sup>	-4617.74	10	9255.61	31.87
	SS + Pros + R + R <sup>2</sup>	-4620.37	8	9256.83	33.08
	SS + M + Pros + R + R <sup>2</sup>	-4619.56	9	9257.21	33.47
	R + R <sup>2</sup>	-4622.63	6	9257.32	33.58
	Pros + R + R <sup>2</sup>	-4622.62	7	9259.31	35.57

**Table A2.4:** Rate of pup feeds (feeds/h)

Model set	Fixed terms	log(L)	d.f.	AICc	$\Delta_i$
(a) Males	ASC + Pros + nPups + aPup + aPup <sup>2</sup> + GS + R	-3319.96	14	6668.05	0.82
	ASC + M + Pros + nPups + aPup + aPup <sup>2</sup> + GS + R	-3318.54	15	6667.22	0.00
	ASC * Pros + M + nPups + aPup + aPup <sup>2</sup> + GS + R	-3315.04	19	6668.31	1.08
	ASC * Pros + nPups + aPup + aPup <sup>2</sup> + GS + R	-3316.45	18	6669.11	1.88
	ASC + M + nPups + aPup + aPup <sup>2</sup> + GS + R	-3321.50	14	6671.13	3.90
	ASC + nPups + aPup + aPup <sup>2</sup> + GS + R	-3323.12	13	6672.35	5.13
	AC + M + Pros + nPups + aPup + aPup <sup>2</sup> + GS + R	-3326.30	14	6680.73	13.50
	AC + Pros + nPups + aPup + aPup <sup>2</sup> + GS + R	-3327.41	13	6680.93	13.71
	AC * Pros + M + nPups + aPup + aPup <sup>2</sup> + GS + R	-3324.01	17	6682.20	14.98
	AC * Pros + nPups + aPup + aPup <sup>2</sup> + GS + R	-3325.11	16	6682.38	15.16
	AC + M + nPups + aPup + aPup <sup>2</sup> + GS + R	-3329.25	13	6684.61	17.39
	AC + nPups + aPup + aPup <sup>2</sup> + GS + R	-3330.52	12	6685.13	17.91
	SS * Pros + nPups + aPup + aPup <sup>2</sup> + GS + R	-3362.01	12	6748.11	80.89
	SS + Pros + nPups + aPup + aPup <sup>2</sup> + GS + R	-3363.76	11	6749.60	82.38
	SS * Pros + M + nPups + aPup + aPup <sup>2</sup> + GS + R	-3361.79	13	6749.69	82.47
	SS + M + Pros + nPups + aPup + aPup <sup>2</sup> + GS + R	-3363.54	12	6751.17	83.95
	SS + nPups + aPup + aPup <sup>2</sup> + GS + R	-3366.31	10	6752.69	85.46
	SS + M + nPups + aPup + aPup <sup>2</sup> + GS + R	-3366.02	11	6754.12	86.90
	Pros + nPups + aPup + aPup <sup>2</sup> + GS + R	-3379.94	10	6779.95	112.72
	nPups + aPup + aPup <sup>2</sup> + GS + R	-3382.29	9	6782.63	115.41
(b) Females	ASC * Pros + aPup + aPup <sup>2</sup> + GS	-3225.48	16	6483.16	0.00
	ASC * Pros + M + aPup + aPup <sup>2</sup> + GS	-3225.47	17	6485.16	2.00
	ASC + Pros + aPup + aPup <sup>2</sup> + GS	-3237.78	12	6499.67	16.52
	ASC + aPup + aPup <sup>2</sup> + GS	-3239.62	11	6501.34	18.18
	ASC + M + Pros + aPup + aPup <sup>2</sup> + GS	-3237.78	13	6501.69	18.53
	ASC + M + aPup + aPup <sup>2</sup> + GS	-3239.62	12	6503.35	20.20
	AC * Pros + aPup + aPup <sup>2</sup> + GS	-3239.62	14	6507.39	24.24
	AC * Pros + M + aPup + aPup <sup>2</sup> + GS	-3239.60	15	6509.37	26.22
	AC + Pros + aPup + aPup <sup>2</sup> + GS	-3248.47	11	6519.04	35.88
	AC + aPup + aPup <sup>2</sup> + GS	-3250.18	10	6520.44	37.28
	AC + M + Pros + aPup + aPup <sup>2</sup> + GS	-3248.44	12	6520.99	37.84
	AC + M + aPup + aPup <sup>2</sup> + GS	-3250.16	11	6522.42	39.26
	SS * Pros + aPup + aPup <sup>2</sup> + GS	-3259.50	10	6539.08	55.92
	SS * Pros + M + aPup + aPup <sup>2</sup> + GS	-3259.36	11	6540.82	57.66

SS + Pros + aPup + aPup <sup>2</sup> + GS	-3264.68	9	6547.42	64.27
SS + aPup + aPup <sup>2</sup> + GS	-3266.49	8	6549.03	65.88
SS + M + Pros + aPup + aPup <sup>2</sup> + GS	-3264.53	10	6549.14	65.98
SS + M + aPup + aPup <sup>2</sup> + GS	-3266.38	9	6550.82	67.67
Pros + aPup + aPup <sup>2</sup> + GS	-3288.70	8	6593.45	110.30
aPup + aPup <sup>2</sup> + GS	-3290.17	7	6594.38	111.22

Number of pups and total rainfall in the past month were excluded from all models for female pup feed rates (b), as these terms did not improve model fits to the data.

**Table A2.5:** Rate of weight gain in pups (g/h)

Fixed terms	log(L)	d.f.	AICc	$\Delta_i$
Pros + Age + nPups + R	-1382.22	8	2780.46	0.30
Pros + Age + nPups + GS + R	-1381.07	9	2780.16	0.00
Pros * GS + Age + nPups + R	-1380.53	10	2781.09	0.92
Pros + Age + nPups * GS + R	-1380.88	10	2781.78	1.62
(Pros + nPups) * GS + Age + R	-1380.41	11	2782.84	2.68
Age + nPups + GS + R	-1386.80	8	2789.62	9.46
Age + nPups + R	-1388.02	7	2790.05	9.89
Age + nPups * GS + R	-1386.87	9	2791.76	11.60