Competition for food in meerkats (*Suricata suricatta)*

By

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Summary

In group living species animals commonly compete for limited resources such as food (Darwin 1859). Winning competition for food may be beneficial for an individuals survival or reproductive success (Williams 1966; Clutton-Brock 1988; Metcalfe *et al* 1995) but conflict with group members may be costly as it typically involves aggression (Huntingford & Turner 1987, Mesterton-Gibbons & Adams 1998). Asymmetries between individuals are predicted to determine the outcome of competition (Maynard-Smith & Parker 1976), and individuals are expected to steal food when the benefit to them is greatest (Barnard 1984; Trivers 1972). I therefore investigate what determines the outcome of competition for food between group members, and what factors affect whether group members try to steal food in the cooperatively breeding meerkat (*Suricatta suricatta*).

Meerkats competed for food items infrequently and the owner of a food item typically won competition, but dominant individuals and breeding females were more likely to win competition than other group members. This provides support for models of conflict over resources in group living species which predict that ownership may determine the

outcome of competition, thereby avoiding frequent costly conflict (Maynard-Smith 1982). Furthermore, where large asymmetries exist between contestants in dominance status or the value of a resource, these may determine the outcome of competition (Maynard-Smith & Parker 1976; Grafen 1987).

Meerkats varied in how frequently they tried to steal food depending upon the costs and benefits of competition. Dominant individuals competed for food more frequently which is likely to reflect reduced costs of competition as subordinate individuals may avoid conflict with them (Packer & Pusey 1985). Females competed for food more frequently than males and more frequently during breeding, reflecting the higher costs of reproduction to females compared to males (Williams 1966; Trivers 1972). Meerkats compete more frequently for food when food availability is low, which indicates that food items may be more valuable when they are rare. Meerkats in smaller groups competed more frequently. In cooperatively breeding species group members undertake a large number of costly helping behaviours. Individuals in small groups each contribute more effort to helping than individuals in large groups and suffer higher costs which may increase the benefit of food to them (Clutton-Brock *et al* 1998a; Clutton-Brock *et al* 2001a).

Competition for the opportunity to breed in cooperatively breeding meerkats has resulted in despotic dominance hierarchies where a dominant female monopolises breeding and reproductively suppresses subordinates (Clutton-Brock *et al* 2001b). Dominant females stole more food than any other group members. This is likely to be a consequence of the high costs of reproduction for the dominant breeding female in species with high reproductive skew (Creel & Creel 1991; Clutton-Brock *et al* 2001b). Furthermore, dominant females were more aggressive and more successful in competition for food with their reproductive competitors. Dominant females may therefore use competition for food as a means of asserting dominance over their reproductive competitors which could contribute to reproductive suppression (Creel *et al* 1992; Williams 2004; Kutsukake & Clutton-Brock 2006b; Young *et al* 2006).

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CHAPTER 1 - *General Introduction*

1.1 Competition for food

Food is a limited resource in the environment which animals therefore compete over (Darwin 1859). Competition for food between group members has been recorded in a range of taxonomic groups including mammals, birds, fish, reptiles and insects (Brockman & Barnard 1979; Ewald & Rohwer 1980; Barnard & Sibley 1981; Barnard 1984; Knight & Knight-Skagen 1988; Borries *et* al 1991; Gommper 1996; Woodroffe & Macdonald 1995). Group members may gain benefits from winning competition for food that contribute to their survival or reproductive success (Williams 1966; Clutton-Brock 1988; Metcalfe *et al* 1995). Contesting a resource, however, may be costly, as competition typically involves aggression (Huntingford & Turner 1987, Mesterton-Gibbons & Adams 1998). Previous research has therefore focused on determining what decides the outcome of competition for food amongst group members (Maynard-Smith 1982) and why they compete for food (Barnard 1984). There has been little study of competition for food that considers differences between group members in the likelihood that they will win and the costs and benefits of competition to them. Furthermore, there has been no study of competition for food in a cooperatively breeding species with high reproductive skew and intense reproductive conflict which may have important consequences for patterns of competition for food. In this study I therefore investigate competition for food in the cooperatively breeding meerkat (*Suricata suricatta*).

1.1.1 Who wins competition for food

Asymmetries between contestants are predicted to decide the outcome of competition for resources (Maynard-Smith & Parker 1976). Such asymmetries are predicted to be (1) in the respective fighting ability of contestants, termed resource holding potential (RHP) (Parker 1974a; Hammerstein 1981); (2) in the resource value (RV) to the two contestants (Parker 1974a; Krebs 1982); or (3) in an aspect of the interaction uncorrelated with the contestants' state such as ownership of a resource (Maynard-Smith & Parker 1976). Costly escalation of contests is expected where individuals have imperfect information regarding asymmetries or where they are equally matched (Safryn & Pellissier Scott 2000). Consequently, distinct predictions can be made about competition for resources in stable group living species in which individuals have prior access to information regarding asymmetries between themselves and other group members (Maynard-Smith 1982; Packer & Pusey 1985). Game theoretical models predict that stable group members may respect asymmetries that decide the outcome of competition for resources avoiding frequent and costly conflict (Maynard-Smith 1982). Typically this will be an asymmetry in dominance status which defines an individuals RHP, but an otherwise uncorrelated asymmetry, such as ownership of a resource, could decide the outcome of competition where the value of a resource is low and costs of conflict are high (Maynard-Smith 1982; Packer & Pusey 1985).

Studies of competition for food in group living species have provided support for these predictions. Furthermore, they indicate that the distribution of food in the environment may be important for determining patterns of competition for food (Wrangham 1980; Warner 1980; Van Schaik 1989). Dominance status commonly correlates with access to food where food resources are localized and of high value (Frank 1986; Borries *et al* 1991; Gompper 1996; Sterck & Steenbeck 1997); ownership of food is important in deciding the outcome of competition where food is widely distributed and of low value (Webster & Hart 2006; Saj & Sicotte 2007). However, these studies have not considered the importance of other possible asymmetries between group members which may also influence the outcome of competition (Grafen, 1987). For example, large asymmetries in RV may overturn an asymmetry in ownership or dominance (Davies & Houston 1981; Krebs 1982; Dill 1983; Morrell *et al* 2005). There have been no studies to date which account for potential variation between group members in dominance status, ownership of a resource, or the value of a resource to individuals. Consequently further investigation is required to determine what asymmetries decide the outcome of competition for food between group members, accounting for all potential asymmetries between group members.

1.1.2 Why do individuals compete for food

Group members may be predicted to compete for food where the benefits are high, which will depend on both the costs of competition for food and the value of food resources to them. Previous research indicates that where group members are more likely to suffer low costs in competition they may compete more frequently, this strategy is commonly adopted by dominant individuals (Barnard 1984; Janson 1987; Saito 1996; Andrade Maura 2003). In some species dominant individuals may even forego self-foraging altogether and operate ‘scrounger’ strategies where they steal from ‘producer’ group members (Barnard & Sibly 1981; Coolen 2002).

Food resources may also be particularly valuable to females as they typically have higher costs of reproduction than males (Williams 1966; Trivers 1972; Hofer & East 2003). Consequently competition for food is predicted to be more intense amongst females than males (Trivers 1972; Wrangham 1980). There is evidence to support these predictions as dominant females steal more food and have higher reproductive success than subordinates in some primates (Borries *et* al 1991; Wittig & Boesch 2003) and the spotted hyena (*Crocuta crocuta*; Hofer & East 2003). However, no study has yet investigated patterns of competition by females in relation to their breeding state.

The benefit of food to individuals is predicted to increase as food availability decreases. Studies investigating temporal changes in food availability have shown that group members compete for food more frequently when there is less food available (Andrade Maura 2003; Saito 1996; Wittig & Boesch 2003). However, these studies have been confined to primates in captivity. Furthermore, it is predicted that in large groups, individuals will compete more intensely for food as they will deplete resources more quickly (Sirot 2000). Further research is therefore required investigating how frequently group members compete for food depending upon food availability and group size.

1.1.3 Reproductive skew, reproductive conflict and competition for food

In some cooperatively breeding species, competition for the opportunity to breed may result in high reproductive skew (Vehrencamp 1983b; Emlen 1991). In such species a dominant male and female typically monopolise reproduction and prevent subordinates from breeding by reproductively suppressing them (Creel *et al* 1992; Keller & Reeve 1994; Creel & Macdonald 1995; Clutton-Brock *et al* 2001b). The resulting asymmetries between group members in reproductive output may have important consequences for competition for food. This is likely to be especially true for the dominant female; reproduction is particularly costly for females in cooperatively breeding species and the dominant female typically has the highest rate of reproduction in the group (Brown 1987; Creel & Creel 1991; Clutton-Brock *et al* 2001b). They may therefore try to steal more food than any other group members.

Reproductive conflict between group members may also have consequences for patterns of competition for food, particularly where reproductive conflict is most intense. Group members could use aggression during competition for food with their competitors as a means of reinforcing their dominance (Kutsukake & Clutton-Brock 2006b), or to deprive them of food resources which may inhibit reproduction (Creel & Creel 1991; Young *et al* 2006). Dominant females commonly show a variety of behavioural tactics that suppress subordinate female reproduction (Choe & Crespi 1997; Faulkes & Abbott 1997; Clark *et* *al* 2001; Young *et al* 2006). Consequently, it is possible that dominant females may use competition for food as an additional tactic in reproductive suppression.

1.1.4 Thesis aims

In this thesis I will use observational and experimental data to investigate patterns of competition for food in a wild population of meerkats. Meerkats are small cooperatively breeding carnivores that live in groups of 3-50 individuals (Clutton-Brock *et al* 2006) and inhabit the semi arid regions of Southern Africa (Skinner and Smithers 1990). Groups are composed of a dominant female and male, and related subordinate adults of both sexes (Griffin *et* al 2003), but may also include subordinate immigrant males unrelated to the dominant female. Subordinates usually delay dispersal from their natal group for 1-3 years into adulthood (O'Riain 2000; Young *et al* 2005) and help with offspring care and other cooperative behaviours (Clutton-Brock *et al* 2001c). There is high reproductive skew amongst both male and female group members (Griffin *et al* 2003) and they compete for the opportunity to breed (Clutton-Brock *et al* 2006). The dominant male and female are responsible for more than 80% of reproduction within the group and reproductively suppress subordinates (Clutton-Brock *et al* 2001b). Consequently dominant females have on average 2.8 litters per year whilst subordinate females only have 0.9 litters per year (Clutton-Brock *et al* 2001b).

Meerkats primarily feed on invertebrates (69% of diet), reptiles (20% of diet), mammals and occasionally amphibians which they excavate from the sandy substrate (Doolan & Macdonald 1996a; Turbe 2006). Foraging group members typically disperse at distances of 1-5m, with a group axis ranging from 20-100m (Doolan & Macdonald 1996a; Barnard 2000). Food items range in size from 0.05g to in excess of 10g, but the majority of food items are small weighing 0.53g on average, although individuals occasionally find larger food items (Brotherton *et al* 2001; Scantlebury *et al* 2002; Turbe 2006). Meerkats can invest extensive effort in excavating food items; holes vary in depth from a few centimeters to up to 50cm in depth. Such excavations may take in excess of 10 minutes to dig and remove up to 8 kg of the substrate (Doolan & Macdonald 1996a, Clutton-Brock *unpublished data*).

Specific aims

In Chapter 3, I undertake a general investigation of what factors decide the outcome of competition for food in a group living species and why individuals compete for food.

In Chapter 4, I investigate whether females compete for food as a result of the benefit of nutritional resources to reproduction. In particular, I investigate whether the high costs of reproduction for dominant females in cooperatively breeding species with high reproductive skew result in them monopolizing food resources in the group.

In Chapter 5, I investigate whether competition for food reflects patterns of reproductive conflict in meerkats. Specifically, I investigate whether competition for food could function as a means of dominance assertion or to deprive competitors of food. Consequently I will consider whether competition for food could contribute to reproductive suppression in cooperatively breeding species.

1.2 Study Species and Study Site

1.2.1 Phylogeny and Distribution

Meerkats (*Suricata suricatta*, Schreber 1776) are group-living, diurnal mongooses belonging to the family *Herpestidae* (formally *Viviridae*) which is comprised of 37 mostly solitary species in 17 genera (Rood, 1986; Veron, 2004). There range extends across the southern African arid zone through Angola, Namibia and South Africa incorporating the southern savanna, karoo and highveldt regions (Skinner and Smithers 1990).

1.2.2 Basic Ecology

Meerkats groups inhabit territories approximately 2-6 Km^2 in size (Turbe 2006; Manser & Bell, 2004). Groups are comprised of a dominant male and female, and numerous subordinate adult males and females of different ages. During the breeding season the group will also have dependent offspring typically born to the dominant male and female (Clutton-Brock *et al* 2001b). Meerkats forage diurnally as a group and rest in subterranean burrow systems at night, and also during the hottest part of the day in the summer season from October to April (Doolan & Macdonald 1996a). Detailed descriptions of foraging behaviour and diet are found in sections 1.1.4 and 1.3.5

1.2.3 Reproduction

Meerkats are obligate cooperative breeders and the dominant male and female monopolise 80% of reproduction within the group (Clutton-Brock 1998; Clutton-Brock *et al* 2001b). Breeding is usually confined to the summer rainy season (Young 2003) when food availability is greatest (Turbe 2006; Doolan & Macdonald 1996a). The dominant female may have up to 4 litters of offspring per year, gestation lasts for approximately 70 days and pups are born in subterranean burrow systems (Doolan & Macdonald 1997b; Clutton-Brock *et al* 2001a; Moss *et al* 2001). Occasionally subordinate females also successfully breed, sometimes simultaneously with either the dominant female or other subordinate females creating mixed litters of offspring of up to 13 pups (Clutton-Brock *et al* 2001b; Clutton-Brock *et al In press*). Pups are entirely dependent on adult care for the first 2-3 months of life. The mother of the pups typically lactates for 45 to 70 days (Clutton-Brock *unpublished data*) but other females in the group may spontaneously allolactate to the pups as well (Doolan & Macdonald 1999). For the first 30 days the pups remain at the breeding burrow and usually 1 to 4 subordinate group members stay at the burrow each day to protect the pups when the group is foraging (Clutton-Brock *et al* 1998a; Clutton-Brock *et al* 2000). Approximately 30 days after birth the pups begin to forage with the group and are provisioned with food items by all group members although the majority of care is provided by the subordinate individuals (Clutton-Brock *et al* 1998a; Russell *et al* 2003). Pups reach independence by approximately 3 months of age (Clutton-Brock *et al* 2001a) and begin helping with subsequent litters of offspring shortly thereafter (Clutton-Brock *unpublished data*).

1.2.4 Dispersal

Males and females usually remain in their natal groups until they are between 1 and 3 years of age. Males leave their own group to go on extra-group forays during the breeding season either individually or as a group of males (Young 2003). They approach other groups where they may mate with receptive subordinate females and occasionally with dominant females (Griffin *et al* 2003). Extra-group forays may last between several hours and several months but males typically return to their own group where they are always accepted back (Griffin *et al* 2003;Young 2003). Extra-group prospecting males may immigrate into groups where there are no adult males or where the number of prospecting males exceeds the number of males in the group (Young 2003). Under these circumstances the immigrating males will depose and evict the resident dominant male (Young 2003). Alternatively, the prospecting males may encounter groups of unrelated evicted females and establish a new group. In contrast, subordinate females do not voluntarily leave their natal group and it appears that the dominant female evicts the older subordinate females from the group during her own pregnancy (Clutton-Brock *et al* 1998b; Clutton-Brock *et al* 2001b; Kutsukake & Clutton-Brock 2006b; Young *et al* 2006). Although evicted females are usually allowed to return to the group after the dominant female has given birth to her pups, they may permanently emigrate if they encounter a group of unrelated prospecting males and establish a new group, especially when several females are evicted simultaneously (Doolan & Macdonald 1997a; Clutton-Brock *unpublished data*). Females never successfully immigrate into established groups. Males and females that immigrate into new groups will either fight for the position of dominance with other individuals that have immigrated with them (Sharpe 2005), or assume dominance when there are no other same-sexed and similarly-aged individuals contesting the position (Hodge *et al* 2008). Both males and females may emigrate from groups they have dispersed into if they have not obtained the dominance position, dominant males will also disperse if the dominant female dies (unrelated to the dominant male) and all other female group members are related to them.

1.2.5 Reproductive conflict and reproductive suppression in meerkats

Strong sexual selection exists on both male and female meerkats (Clutton-Brock *et al* 2006). There are limitations on the opportunity for meerkats to breed within a group (Clutton-Brock 1998; Clutton-Brock 2001b), and consequently there is high reproductive skew amongst meerkats of both sexes and extensive competition for access to reproduction (Clutton-Brock *et al* 2006). Subordinate group members aggressively compete for the opportunity to become dominant, either fighting with the dominant individual in the group in an attempt to displace them, or fighting with other same sex subordinate individuals for the dominance position when it becomes available. On occasion, injuries from these fights can be fatal and the losing competitor may be forced out of the group (*Personal observation*). The eldest individual almost invariably wins, but in females, where individuals competing are of the same age it is usually the larger one that wins the position of dominance (Hodge *et al* 2008).

The dominant male and female of the group regularly assert dominance over subordinate individuals and prevent them from breeding (Clutton-Brock *et al* 2005; Kutsukake & Clutton-Brock 2006b; Clutton-Brock *et al* 2006; Kutsukake & Clutton-Brock *In press*). The dominant male frequently aggresses against other males in the group that are unrelated to the dominant female, and will follow the dominant female intently during her oestrus period preventing other males from gaining access to, and trying to mate with her (Griffin *et al* 2003; Kutsukake & Clutton-Brock *In press*). The dominant female frequently aggresses against the subordinate females in the group particularly the older females who more frequently become pregnant than younger subordinates (Kutsukake & Clutton-Brock 2006b; Hodge *et al In press*). When the dominant female is pregnant she increases the frequency of aggression against subordinate females and forcibly evicts the older subordinate females and any pregnant females from the group (Kutsukake & Clutton-Brock 2006b; Young *et al* 2006). Evicted females suffer from high levels of stress and typically fail to conceive or abort any pregnancies (Young *et al* 2006). If subordinate females give birth to pups when the dominant female is pregnant, the dominant female will kill the pups (Clutton-Brock *et al* 1998b; Young *et al* 2006). Pregnant subordinate females will also kill any pups born to other females in the group (including the dominant females), and consequently eviction may also function to minimise infanticide of the dominant females offspring (Young & Clutton-Brock 2006).

1.3 Study Site

1.3.1 Location

The study was undertaken on an area of approximately 70 km² incorporating the Kuruman River Reserve and surrounding ranch land. The site is located in the Southern Kalahari Desert in South Africa (26°59’ S, 21°50’ E), approximately 15km south of the Botswana border (Fig 2.1)

Figure 1.1. Location of the study site in South Africa as indicated by the hatched box.

1.3.2 Climate

The Southern Kalahari is a semi arid region with distinct hot, wet summer and cold, dry winter seasons (Mills 1990). Daily rainfall and maximum/minimum temperature were recorded at the study site from 1998 to 2007 using a rain gauge and mercury thermometer. The summer season runs from October to April; between October and April from 1998 to 2007 average daily minimum and maximum temperatures were 18°C and 34°C respectively and average monthly rainfall was 40 mm. The winter season runs from May to September; between May and September from 1998 to 2007 average daily minimum and maximum temperatures were 6°C and 24°C respectively and average monthly rainfall was 5 mm. Figure 1.1.a and 1.1.b show the average monthly minimum and maximum temperatures and the average monthly rainfall from January 1998 to April 2007

Figure 1.2.a. Average monthly minimum and maximum temperature (°C) between January 1998 and April 2007 on the Kuruman River Reserve.

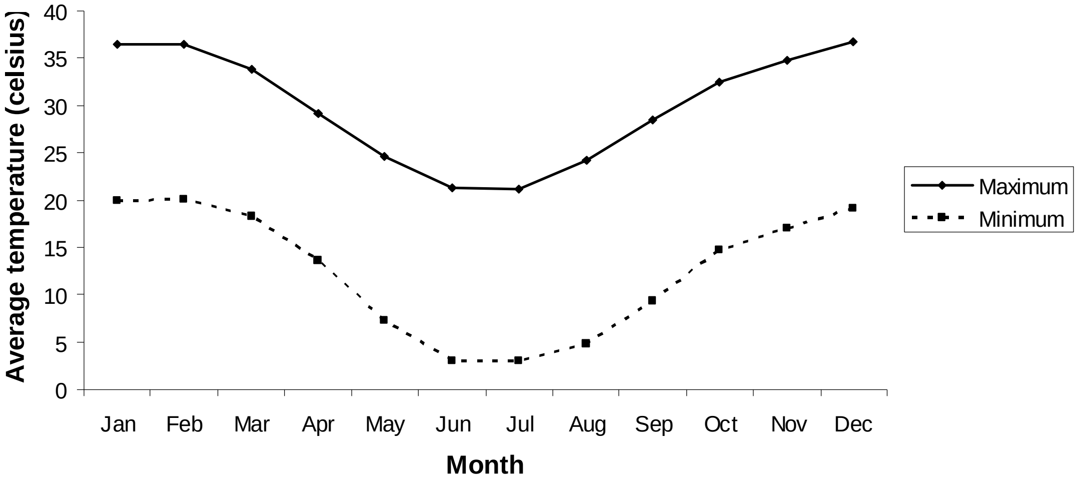
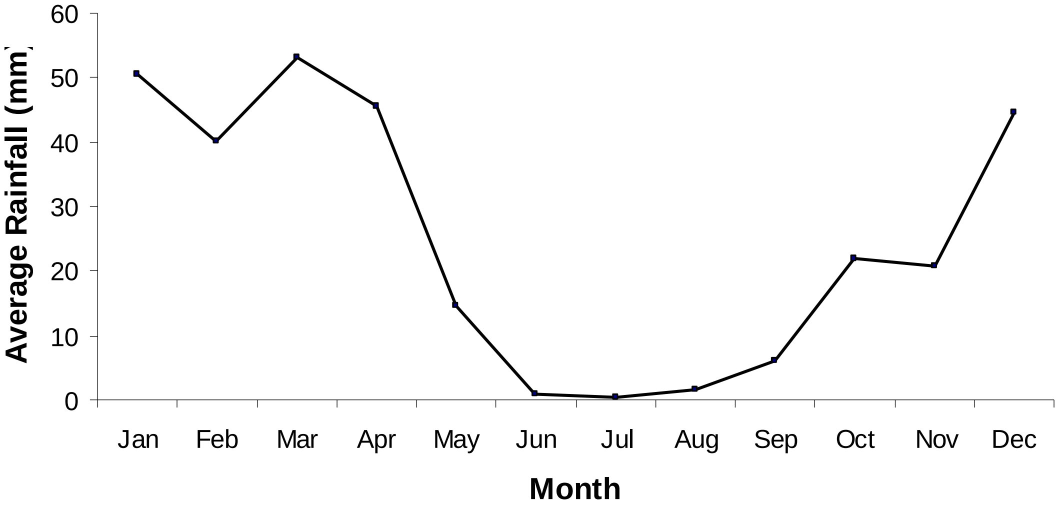


Figure 1.2.b. Average monthly rainfall (mm) between January 1998 and April 2007 on the Kuruman River Reserve.



1.3.3 Habitat

The study site was typified by Kalahari thornveld (Leistner & Werger 1973), and was bisected by the dry bed of the Kuruman River. Flat terraces and low shrubby dunes adjoined the dry river bed giving way to low sparsely vegetated dunes away from the riverbed (Rooyen *et* al 1991). Vegetation on the flat terraces and shrubby dunes adjacent to the river bed were characterised by low shrubs including *Rhigozum* trichotomu and *Monechma spp*., bushes and trees including Camel thorn acacia, *Acacia erioloba*, Grey camel thorn acacia, *Acacia haemotoxylon*, Buffalo thorn, *Ziziphus mucronata*, Black thorn, *Acacia mellifora*, Velvet raison bush, *Grewia flava* and Shepard's tree *Boscia albirtunca*, but also the introduced glandular mesquite, *Prosopis* glandulosa. Vegetation on the rolling dunes low dunes away from the riverbed was typified by perennial grasses including *Aristida, Eragrostis, Stipagrostis and Schmidtia Spp*. but also occasional trees and bushes, predominantly Camel thorn acacia, *Acacia erioloba*, Grey camel thorn acacia, *Acacia haemotoxylon*, Buffalo thorn, *Ziziphus mucronata and* Velvet raison bush, *Grewia flava*. The ranch land and Kuruman River Reserve have suffered from extensive overgrazing by stock over the last century, specifically by cattle, sheep and goats. Large naturally occurring herbivores at the study site included steenbok (*Raphicerus campestris*) common daika (*Sylicapra grimmia*), springbok (*Antidorcus marsupialis*) and gemsbok (*Oryx gazelle*); since 2002 populations of blue wildebeest (*Connochaetes taurinus*), red hartebeest (*Alcelaphus buselaphus*) and eland (*Taurotragus eland*), have been reintroduced to the Kuruman River Reserve.

1.3.4 Predators

Although the diversity and number of predators at the study site has been reduced by human activity, meerkats are still vulnerable to predation. The resident predators include; the mammals, caracal (*Felis caracal*), wild cat (*Felis libyca*), jackal (*Canis mesomelas*), cape fox (*Vulpes chama*), slender mongoose (*Herpestes sanguineus*), yellow mongoose (*Cynictis pencillata)*, domestic cats (*Felis domesticus*) and domestic dogs (*Canus familiaris*); numerous predatory bird species, including, marshall eagle (*Polemaetus bellicosus*), tawny eagle (*Aquila rapax*), black breasted snake eagle (*Circaetus gallicus*), brown snake eagle (*Circaetus cinereus*), jackal buzzard (*Buteo rufofuscus*), steppe buzzard (*Buteo vulpinus*), pale chanting goshawk (*Meliarax canorus*), Verreux's giant eagle owl (*Buba lacteus*) and spotted eagle owl (*Buba africanus*); and several reptiles including rock monitor (*Varanus exanthematicus*), cape cobra (*Naja nivea*), puff adder (*Bitis arietans*) and mole snake (*Pseudaspis cana*).

1.3.5 Food

Meerkats are carnivorous and forage for food items buried beneath the sand; they search continuously for potential hidden prey or holes by scratching the surface as they slowly move forward, and excavate food items they locate by digging with their forearms. They are capable of excavating in excess of 8kg of substrate in 10 minutes going to depths of over 50 cm in search of food items (Earthwatch unpublished data). Food items typically range in size from 0.1g to 10g and include insects, insect larvae, Chelicerates, rodents, small reptiles and amphibians (further details may be found in Doolan & Macdonald 1996a and Brotherton *et al* 2001). The availability of meerkat food prey strongly correlates with recent rainfall (Seely & Louw 1980; Pianka 1986; Doolan and Macdonald 1996a; Barnard 2000; Turbe 2006), and is greatest in the hot, wet summer (October to April) and least in the cold, dry winter (April to September), (Doolan & Macdonald 1996a; Turbe 2006)

CHAPTER 2 - *Competition for Food in a Cooperatively Breeding Species, the Meerkat (Suricata suricatta).*

ABSTRACT

In group living species individuals commonly compete for food resources. Food may be beneficial for survival or reproductive success but conflict may be costly. Consequently group members are predicted to show respect for an asymmetry that decides the outcome of competition, thereby avoiding frequent conflict. In this study, competition for food by the cooperatively breeding meerkat (*Suricata suricatta*) was investigated to consider what asymmetries between group members decide the outcome of competition, and which factors affect whether individuals compete. It is shown that ownership of a food item typically decides the outcome of competition and therefore may be a respected asymmetry between group members. However, large asymmetries in dominance status resulting from competition for the opportunity to breed also affected the outcome of competition food. Consequently, dominant individuals were able to steal more food.

Individuals varied how frequently they tried to steal food depending upon the costs and benefits of competition for food. This analysis improves our understanding of how conflict is avoided in group living species and why group members compete for food resources. It also provides evidence that competition for the opportunity to breed in cooperatively breeding species may have, consequences for competition for food.

2.1 INTRODUCTION

Animals commonly compete for limited resources such as food, particularly in group living species. Winning competition for food may be beneficial for survival or reproductive success (Williams 1966; Clutton-Brock 1988; Metcalfe *et al* 1995), but contests may also be costly as competition typically involves aggression (Huntingford & Turner 1987, Mesterton-Gibbons & Adams 1998). Consequently group members may have some means of determining or predicting who wins competition for food (Maynard-Smith 1982). Furthermore, the extent of competition for food is likely to vary depending upon the costs and benefits of competition to different individuals. This study will therefore investigate two main questions; what decides the outcome of competition for food between group members; and why do group members compete for food in a cooperatively breeding species, the meerkat (*Suricata suricatta*).

What decides the outcome of competition for food in group living species

Game theoretical models predict that in stable group-living species, individuals will use information regarding asymmetries with other group members to decide the outcome of competition, avoiding frequent and costly conflict (Maynard-Smith 1982). The asymmetries they are predicted to respect are in dominance status, which may define an individuals fighting ability or resource holding potential (RHP; Parker 1974a; Hammerstein 1981, Packer and Pusey 1985); or in an arbitrary asymmetry such as ownership of a resource, especially where the costs of conflict are high or the benefits are low. (Maynard-Smith 1982; Packer & Pusey 1985). Empirical evidence supports these predictions (Nishida 1979; Engvist & Leimer 1990; Gompper 1996; Hofer & East 2003; Hodge *et al* 2007).

In addition the distribution of food resources is important in determining whether dominance or ownership decides the outcome of competition (Wrangham 1980). Where the opportunity to compete for food is common and the value of food items is high, dominance status typically decides the outcome of competition (Imanishi 1960; Watts 1985; Frank 1986; Janson 1987; Borries *et al* 1991; Gompper 1996; Hofer & East 2003). Conversely, where food is more widely dispersed in the environment and of lower value, group members compete for food infrequently (Webster & Hart 2006), and show respect for ownership of a food resource in competition (Saj & Sicotte 2007). However, these studies do not account for other potential asymmetries between group members that may be of some importance in deciding the outcome of competition for food between specific group members.

Where an asymmetry between individual competing group members is large, these may superce other asymmetries which more typically decide the outcome of competition for a resource (Grafen, 1987). For example, an asymmetry in dominance status could overturn a typically respected asymmetry in ownership of a resource (Beaugrand *et al* 1996; Cutts *et al* 1999; Johnsson *et al* 1999). In species with large asymmetries in dominance status between group members, subordinate individuals may avoid costly conflict with dominants (Huntingford & Turner 1987). This may occur as a result of asymmetries in fighting ability (RHP) between dominant and subordinate individuals (Maynard-Smith & Parker 1976; Packer & Pusey 1985). Consequently, the costs of conflict may be lower for dominant individuals in competition for food and so they may initiate competition for food more frequently. In some species, dominant group members that are likely to win in competition for food have been shown to operate a ‘scrounger’ strategy if the payoffs to taking food from ‘producers’ rather than foraging are high (Barnard & Sibley 1981). Where the opportunity to monopolize food is comparatively rare, a scrounger strategy may not make a significant contribution to an individuals total food intake and competition for food is consequently likely to be rare (Wrangham 1980; Barnard 1984).

Why do group members compete for food resources

Food resources may vary in their value to individual group members. When food resources are more valuable to particular group members, they may try to steal more food. Food is typically a major limitation on female reproductive success (Williams 1966), particularly in cooperatively breeding species (Creel & Creel 1991), and females are therefore predicted to compete for food resources more than males (Trivers 1972). Studies of competition for food by female group members indicate that they may compete more intensely for food than males, and group members that are more successful in competition for food also have the highest reproductive success (Borries *et al* 1991; Hofer & East 2003). Food may additionally become more valuable when its availability in the environment is reduced. Studies investigating temporal changes in food availability have shown that the frequency of competition for food by all group members increases as available food availability decreases (Andrade Maura 2003; Saito 1996; Wittig & Boesch 2003). Furthermore, large groups are predicted to deplete food resources more than smaller groups, and may therefore show increased conflict over food (Sirot 2000; Koenig 2002; Saj & Sicotte 2007). Whilst studies have considered why group members compete for food, few have considered the effect of variation in the costs and benefits on competition for food to specific group members. Furthermore, those that have were undertaken on captive species (Andrade Maura 2003; Saito 1996). Consequently there is an opportunity to investigate why specific group members compete for food in a free living population of animals.

This study investigates which factors affect the outcome of competition for food and the frequency with which individuals initiate competition for food in a free living population of meerkats (*Suricata suricatta*). Meerkats are small cooperatively breeding carnivores that live in groups of 3-50 individuals (Clutton-Brock *et al* 2006) and inhabit the semi-arid regions of Southern Africa (Skinner and Smithers 1990). Groups are composed of a dominant male and female who are responsible for more than 85% of reproduction within the group (Griffin *et al* 2003), and subordinate adults who are typically the offspring of the dominant female and male. Subordinates usually delay dispersal from their natal group for 1-3 years into adulthood (O'Riain 2000; Young *et al* 2005) and help with offspring care and other cooperative behaviours (Clutton-Brock *et al* 2001c).

Consequently meerkat groups are composed of a large number of individuals of different dominant status, size, age and sex.

Meerkats are carnivores that primarily feed on invertebrates (69% of diet), reptiles (20% of diet), mammals, and occasionally amphibians which they excavate from the sandy substrate (Doolan & Macdonald 1996a; Turbe 2006). Foraging group members are dispersed at distances of 1-5m, with a group axis ranging from 20-100m (Doolan & Macdonald 1996a; Barnard 2000; Turbe 2006). Food items range in size from 0.05g to in excess of 10g, the majority of food items are small weighing an average of 0.53g, although individuals occasionally find larger food items (Brotherton *et al* 2001; Scantlebury *et al* 2002; Turbe 2006). Meerkats can invest extensive effort in excavating food items; holes vary in depth from a few centimeters to up to 50cm in depth. Such excavations may take in excess of 10 minutes to dig and remove 8 kg of the substrate (Doolan & Macdonald 1996a, Clutton-Brock *unpublished data*).

Analyses will first be undertaken to investigate what asymmetries between group members decide the outcome of competition for food. In particular, the study will consider whether group members may respect asymmetries in ownership of a resource. Secondly, the study will investigate how the frequency of competition for food by different group members varies in response to the costs and benefits of competition for food to them.

2.2 METHOD

2.2.1 Study Population

Data were collected on a free ranging population of meerkats living on ranchland located in the Southern Kalahari desert in South Africa (26°59’ S, 21°50’ E), approximately 15km south of the Botswana border. The area experienced two distinct seasons; a hot, wet ‘summer’ from October to April and cold, dry ‘winter’ from May to September (Mills 1990, Doolan & Macdonald 1996a, Clutton-Brock *et al* 1999a). Further details of the ecological conditions and climate at the study site may be found elsewhere (Russell *et al*

2002). During the study period there were between 8 and 14 groups of meerkats comprising 150 to 300 meerkats under observation at any one time. In total over 27 groups were observed comprising 810 adult (>12 months of age) individuals. All individuals were habituated to close observation at distances of less than 2 metres while foraging. One adult individual in each group was fitted with a radiocollar and the groups could therefore be easily located. Individual meerkats were instantly recognisable by unique dye marks on their fur and a unique transponder chip was inserted under the skin at the base of the neck of all individuals when they were 20 to 30 days of age to ensure a permanent record of identity. All groups in the population were visited at least every 3 days enabling the accurate collection of life history information for all individuals in the population (e.g. births, deaths, dispersal etc) and group composition. Consequently the age of 95% of the population was known to within 3 days: for the purpose of this study all analyses were restricted to adult individuals. The weight of each meerkat could be obtained without capture by placing a small egg reward (<1g) on an electronic scale which the meerkats would then obtain by climbing onto the scale. Weights were collected at groups during the morning before the group had begun foraging (morning weight) and at lunch following a prolonged foraging period of no less than 2 hours (lunch weight). The 'rate of morning weight gain' could then be calculated (lunch weight – morning weight / foraging time). Rainfall at the study site was measured daily (to the nearest mm); rainfall strongly correlates with food abundance in the southern Kalahari (Seely & Louw 1980; Pianka 1986; Doolan and Macdonald 1996a; Barnard 2000; Turbe 2006). Consequently the average daily rainfall (mean rainfall per day) over an observation period or the total rainfall over a three month period (where appropriate) were fitted in analyses to control for food availability.

2.2.2 Data Collection

Behavioural observations of each meerkat group were undertaken during the morning for approximately three hours and in the evening for approximately 1.5 hours, three days each week from May 1998 to May 2007. Behavioural data were collected *Ad libitum* (Altmann 1974) and recorded on hand held Psion® data recorders. Competition for food is defined as a dyadic contest ‘event’ between adult individuals over a single food item, where an ‘initiator’ attempted to take a food item from an ‘owner’. Initiation was described as approaching a foraging individual or individual with a food item to a distance of <50cm whilst looking at the owner’s hole or food item and not foraging or undertaking any other behaviour. The initiator’s subsequent level of aggression toward the owner was classed either as ‘no contact’ where it approached the owner but did not make contact (the owner would typically growl and/or block access to the food item); or as ‘contact’ when it made contact with the owner either by pushing against them to try and obtain the hole or food item, or by physically attacking and biting them. The outcome of competition for a food item was recorded as either the initiator ‘winning’ or ‘losing’ competition with an owner for a hole/food item. The initiator was classed as winning when it took part or all of a food item or hole from the original owner and was otherwise classed as losing. Food items were also classified by size as either; ‘hole’, where an initiator competed for another group members excavation in progress prior to food being found; ‘small’, requiring between 1 and 15 chews to consume with less than 50% of the food item protruding from the mouth; or ‘large’, requiring >15 chews to consume and with greater than 50% of the food item protruding from the mouth.

To investigate what factors influence how frequently individual meerkats tried to steal food items and how successful they were in doing so, a single measure of each individuals ‘frequency of initiation’ (total number of observed initiations divided by total observation time) and ‘success in competition’ (total number of ‘wins’ by an initiator divided by total number of initiations) was calculated for each summer (October to April) and winter (May to September) ‘observation period’ throughout the study. Whenever the state of the individual changed during a summer or winter season separate measures of frequency of initiation, and success in competition were calculated, resulting in separate observation periods corresponding to the time an individual spent in each different state during a season. Individuals could change with respect to breeding state (pregnant, lactating, not breeding), dominance status (dominant, subordinate), or immigrant status (immigrant or subordinate). For the purpose of this study, pregnant and lactating females, immigrant subordinates and dominant males in their natal groups were excluded from analyses. In addition, where the total observation time during an observation period was less than 10 hours, the period was excluded from any analysis. Each individual's average age (mean number of days), average morning weight (grams; mean, excluding calculations based on less than 5 morning weights), average morning rate of weight gain (grams; mean, excluding calculations based on less than 5 rates of morning weight gain), were calculated for each observation period. To control for any effects of group size, average group size during an observation period (mean number of foraging individuals >3 months of age) was fitted as a variable in all analyses. Average daily rainfall during observation period (mm) was also included to control for the effect of food availability.

All research protocols were approved by the University of Pretoria ethics committee and conform to the Association for the Study of Animal Behaviour guidelines for the use of animals in research.

2.2.3 Statistical Analysis

All statistical analyses were conducted using Genstat 9.1 (Lawes Agricultural Trust, Rothamsted, Harpenden, UK). Where multivariate analyses involved repeated sampling of groups or individuals, General Linear Mixed Models (LMMs) and Generalised Linear Mixed Models (GLMMs) were used. These are similar to General and Generalised Linear Models, but allow both fixed and random terms to be included. In all mixed models, variance components were estimated using the Restricted Maximum Likelihood (REML) method, and random terms were retained in the model unless the variance component was found to be zero. Where terms correlated (e.g. age and weight), the inclusion of both in the model could lead to spurious measures of significance (Grafen & Hails 2002; Quinn & Keough 2002). Consequently the term that had a lesser effect was excluded from analysis. In each model, all potential explanatory terms were entered together and then dropped sequentially until only those terms that explained significant variation remained. Repeating the analysis by successive inclusion of significant terms to build a minimal model using the additive method yielded an identical final model in all cases. Each dropped term was then put back into the minimal model to obtain their level of non-significance and to check that significant terms had not been wrongly excluded. All two-way interactions were tested, but were only presented if found to explain significant variation. All statistical tests were two-tailed. Where data differed significantly from normality (based on the Anderson-Darling test for normality) data were transformed to obtain normality or otherwise non-parametric statistics were used. Where Wilcoxon Matched Pairs Signed-Ranks tests were used medians and Inter Quartile Ranges (IQRs) are reported.

2.2.4 Factors that affect the outcome of competition for food

To determine the factors that affect the outcome of competition for food, the proportion of occasions the initiator of competition successfully stole a food item was investigated. Success in competition for food by dominant males, dominant females, subordinate females and subordinate males was tested against a percentage success of 50% as may be expected by chance, using a Wilcoxon signed rank test. To obtain one value for success rate for each dominance and sex class in each group, the success rates of all subordinate males and all subordinate females in a group were averaged (there was only ever one dominant male and female in each group). Data were restricted to competition for food initiated by individuals between March and October 2003, a period during which group composition and the dominant individuals in the population remained comparatively stable (less than two individuals disappeared from any group). Measures of success in competition for food by individuals that either disappeared or changed dominance status were excluded from the analysis. This resulted in measures of success for 12 dominant females, 12 dominant males, 9 subordinate females and 9 subordinate males.

To investigate what aspects of the initiator of competition for food and the owner of a food item decide the outcome of competition, a GLMM was used to assess what factors affect whether the initiator of competition for food successfully stole a food item from the owner. Data were available for 3602 competitions for food, initiated by dominant and subordinate individuals of both sexes. Whether the initiator of competition for a food item won (1) or not (0) was set as the binomial response term in a GLMM with 1 as the binomial denominator. The following factors and variables were incorporated as possible explanatory terms: dominance status and sex of both the initiator and owner; weight difference between initiator and owner (g; calculated by subtracting the morning weight of the initiator from the owner); and size of food item (hole, small, large). Group size on the day and rainfall (total rainfall during the previous 3 months) were also included to control for any effect they may have. Repeated measures within group, initiator and owner were controlled for by including them as random terms.

2.2.5 Factors that affect the frequency of competition for food

To determine the factors that affect individual motivation to initiate competition for food, it was necessary to conduct two separate analyses as the frequency of initiation by individuals was commonly 0. First a GLMM was used to investigate what factors affect whether an individual competed for food or not during an observation period. Data were available for dominant and subordinate individuals of both sexes, incorporating 2002 observation periods on 682 individuals at 24 different groups. Whether an individual competed for food during an observation period (1) or not (0) was set as the binomial response term in a GLMM with 1 as the binomial denominator. The following factors and variables were included as possible explanatory terms: sex, dominance status, and average weight of initiator (g). The total observation time (mins) for that individual during the period in question, average group size, and rainfall in observation period (factorised as high or low around the mean average rainfall) were also included to control for any effect they may have. Repeated measures of group and individual were included in the model as random terms.

A LMM was then used to undertake a more detailed analysis, investigating what factors affect the frequency of initiation by individuals that had competed at least once during an observation period. Data were available for dominant and subordinate individuals of both sexes, incorporating data from 1115 observation periods on 525 individuals at 23 different groups. Frequency of initiation was logarithmically transformed and set as the response term in a LMM. The factors and random terms were identical to those in the model outlined above and residuals from the model were normally distributed.

2.3 RESULTS

2.3.1 *Factors that affect the outcome of competition for food*

Overall, the initiator of competition for a food item was successful in only 12% ±23% (mean, S.D.) of interactions. Initiators of competition for food had a significantly lower likelihood of success than may be expected by chance (50%) irrespective of the initiating individuals dominance status or sex; dominant females (Median = 28.05, IQR = 18.24 – 35.59; $W = 0$, $n = 12$, $P = 0.003$); dominant males (Median = 19.37, IQR = 2.08 – 27.08; $W = 0$, $n = 12$, $P = 0.003$); subordinate females (Median = 6.10, IQR = 0 – 11.81; $W = 0$, $n = 9$, $P = 0.009$); and subordinate males (Median = 4.17, IQR 0 – 13.14; $W = 0$, $n = 9$, $P = 0.009$). Therefore, the owner of a food item was more likely to win competition for food. However, dominant individuals initiating competition were more likely to win competition for food than subordinate individuals (GLMM: $\chi^2_1 = 30.94$, $P = <0.001$; Table 2.1; Fig. 2.1.a) and less likely to lose when they were the owner of a food item (GLMM: $\chi^2_2 = 14.10$, $P = <0.001$; Table 2.1). There was a significant interaction between the sex and dominance status of the owner of a food item indicating that whilst dominant females were less likely to lose in competition for food than dominant males when they were the owner of a food item, subordinate females were more likely to lose than subordinate males (GLMM: $\chi^2 = 13.80$, $P = <0.001$; Table 2.1; Fig. 2.1.b). The initiator of competition was more likely to win competition for large food items and holes than competition for small food items (GLMM: $\chi^2_2 = 10.60$, $P = <0.005$; Table 2.1; Fig. 2.1.c). Weight differences between competing individuals had no effect on the outcome of competition for food (GLMM. $\chi^2_4 = 0.20$, $P = 0.659$; Table 2.1).

Table 2.1. GLMM (with a binomial distribution and a logit link function) of the terms affecting the likelihood that an initiating individual successfully stole a food item from the owner

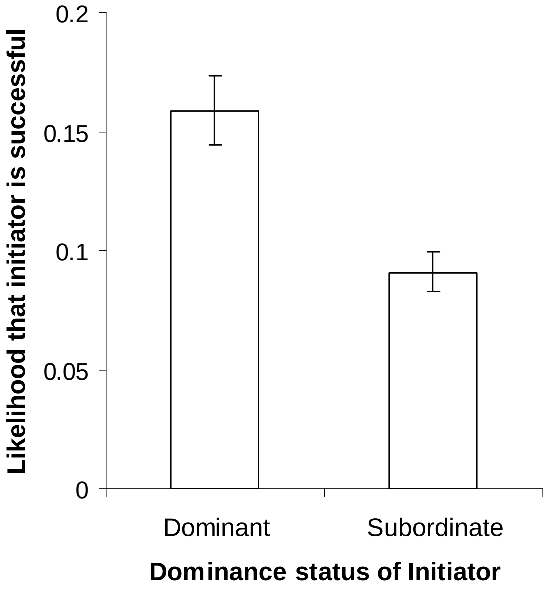
Full model	**Wald statistic (χ^{2})**	**d.f**	***P***

Initiator dominance status		30.94	1	<0.001
Owner dominance status		13.84	1	<0.001
Owner dominance status * owner sex		13.80	1	<0.001
Food size (hole, small, large)		10.60	2	0.005
Rainfall (mm)		2.40	1	0.12
Owner sex		1.31	1	0.25
Group size		0.38	1	0.54
Initiator sex		0.30	1	0.58
Weight difference (g)		0.20	1	0.66
Minimal model		**Effect**	**S.E.**	
Constant		-2.04	0.16	
Initiator dominance status	Dom	0.00	0.11	
	Sub	-0.63	0.10	
Owner dominance status	Dom	0.00	0.11	
	Sub	0.78	0.10	
Owner dominance status * owner sex		See Fig. 2.1.b		
Food size	Hole	0.00	0.11	
	Small	-0.27	0.13	
	Large	0.17	0.11	

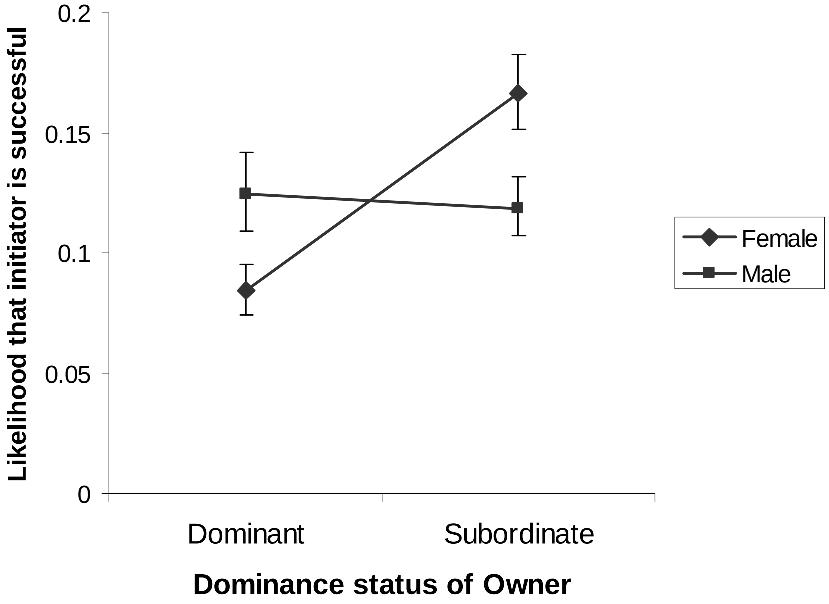
Group (component±SE=0.05±0.04), and initiator (0.05±0.06) were included as random terms in the model.

Fig. 2.1. The affect of (a) initiator dominance status (b) the dominance status of male and female owners of a food item and (c) food item size, on the likelihood that the initiator of competition for food will successfully steal a food item from its owner. All graphs show predicted means and standard errors from a GLMM controlling for the effects of significant terms and random terms listed in Table 2.1.

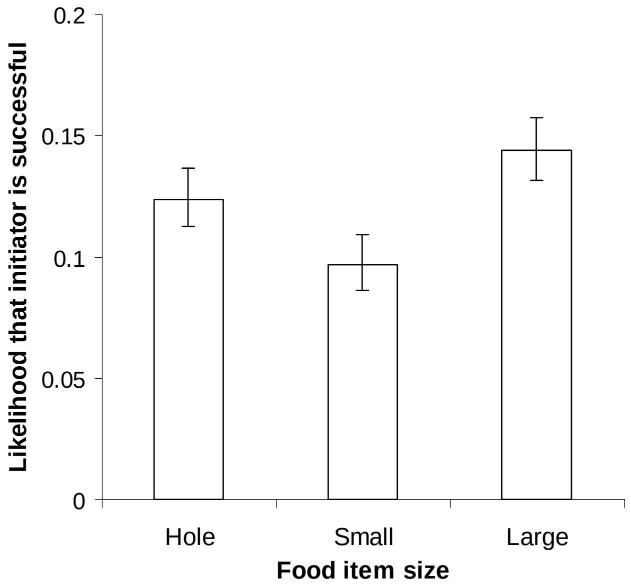
(a)



(b)



(c)



2.3.2 Factors that affect the frequency of competition for food

The mean rate of competition for food per hour by subordinate females was 0.017 ±0.029 events/hr; subordinate males 0.013 ±0.021 events/hr (mean, S.D.); dominant males 0.038 ±0.056 events/hr; and dominant females 0.065 ±0.087 events/hr. In the first analysis, dominant individuals were more likely to initiate competition for food at least once during an observation period than subordinates (GLMM: $\chi^2_1 = 40.06$, $P = <0.001$; Table 2.2; Fig. 2.2.a), after controlling for the significant positive effect of total observation time. Furthermore, females were more likely to initiate competition for food than males (GLMM: $\chi^2_2 = 8.75$, $P = 0.003$; Table 2.2; Fig. 2.2.b) and lighter individuals were more likely to initiate competition than heavier individuals (GLMM: $\chi^2_4 = 21.95$, $P = <0.001$; Table 2.2; Fig. 2.2.c). When rainfall during an observation period was low individuals were more likely to initiate competition for food than when rainfall was high (GLMM: $\chi^2 = 24.46$, $P = <0.001$; Table 2.2; Fig. 2.2.d). Individuals in small groups were more likely to initiate competition for food during an observation period than individuals in larger groups (GLMM: $\chi^2 = 11.41$, $P = <0.001$; Table 2.2; Fig. 2.2.e). Furthermore, there was a significant interaction between group size and rainfall; individuals in small groups were more likely to initiate competition for food when rainfall was high during an observation period compared with individuals in large groups (GLMM interaction: $\chi^2 = 15.47$, $P = <0.001$; Table 2.2; Fig. 2.2.f).

These results were supported by a second analysis of what factors affected the actual frequency at which individuals initiated competition for food. Dominant individuals initiated competition for food more frequently than subordinates (LMM: $\chi^2_1 = 180.56$, $P = <0.001$; Table 2.3), and females initiated competition for food more frequently than males (LMM: $\chi^2 = 24.42$, $P = <0.001$; Table 2.3). Furthermore, dominant females initiate competition for food more frequently relative to dominant males than subordinate females did relative to subordinate males (LMM interaction term: $\chi^2_3 = 11.89$, $P = <0.001$; Table 2.3; Fig. 2.3.a). When rainfall was low during an observation period individuals initiated competition for food more frequently (LMM: $\chi^2 = 5.41$, $P = 0.020$; Table 2.3), and when group size was small during an observation period, individuals initiated competition for food more frequently (LMM: $\chi^2 = 32.29$, $P = <0.001$; Table 2.3). In addition, individuals in large groups initiated competition for food less frequently when rainfall was high during an observation period whilst individuals in small groups did not differ in how frequently they initiated competition for food when rainfall was high or low (LMM: $\chi^2 = 11.89$, $P = <0.001$; Table 2.3; Fig. 2.3.b).

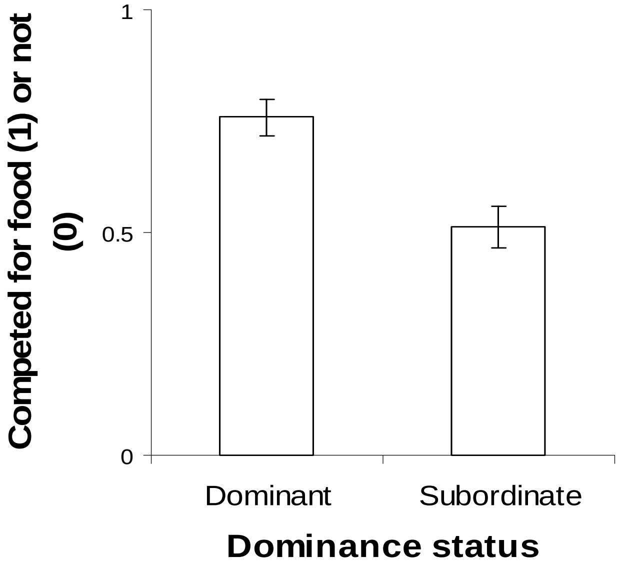
Table 2.2. GLMM (with a binomial distribution and a logit link function) of the terms affecting the likelihood that an individual competed for a food item at least once during an observation period.

Full model		**Wald statistic (χ^2)**	**d.f**	***P***
Total observation time (mins) ψ		136.66	1	<0.001
Dominance status		40.06	1	<0.001
Rainfall (high, low)		24.46	1	<0.001
Weight (g)		21.95	1	<0.001
Group size * rainfall		15.47	1	<0.001
Group size		11.41	1	<0.001
Sex		8.75	1	0.003
Minimal model		**Effect**	**S.E.**	
Constant		1.054	0.25	
Dominance status	Dom	0.00	0.23	
	Sub	-1.10	0.19	
Sex	Female	0.00	0.21	
	Male	-0.37	0.20	
Weight		-0.01	0.01	
Rainfall	High	0.00	0.32	
	Low	0.57	0.89	
Group size		-0.08	0.01	
Group size * rainfall		See Fig. 2.2.f		
Minutes observation ψ		0.0001872	0.00001601	

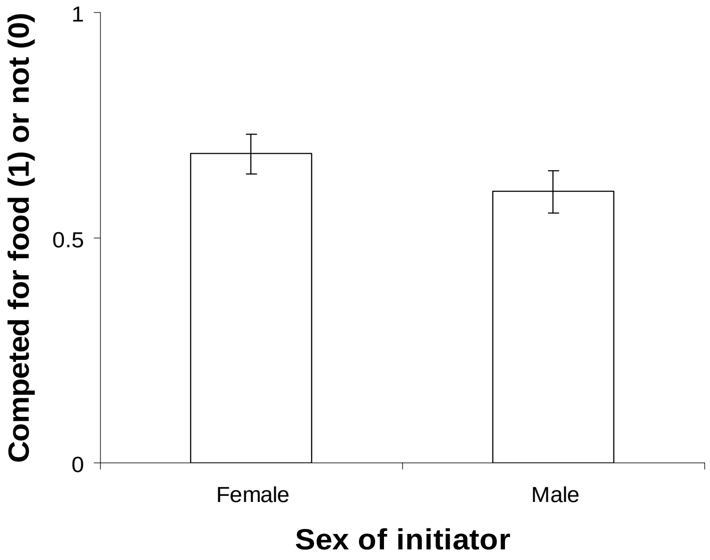
Group (component±SE=0.49±0.22), and initiator (0.30±0.12) were included as random terms in the model.

Fig. 2.2. The affect of (a) initiator dominance status (b) initiator sex (c) initiator weight (d) rainfall (e) group size and (f) high or low rainfall for groups of different sizes, on the likelihood that an individual competed for food during an observation period. All graphs show predicted means and standard errors or lines of best fit generated from a GLMM controlling for the effects of significant terms and random terms listed in Table 2.2.

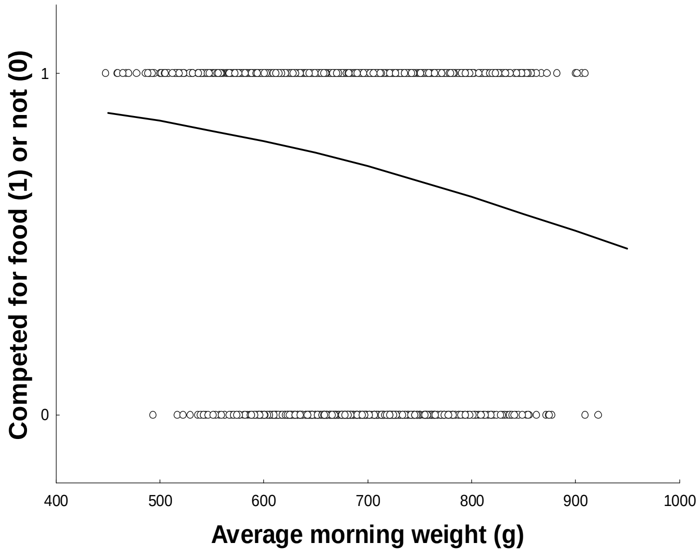
(a)



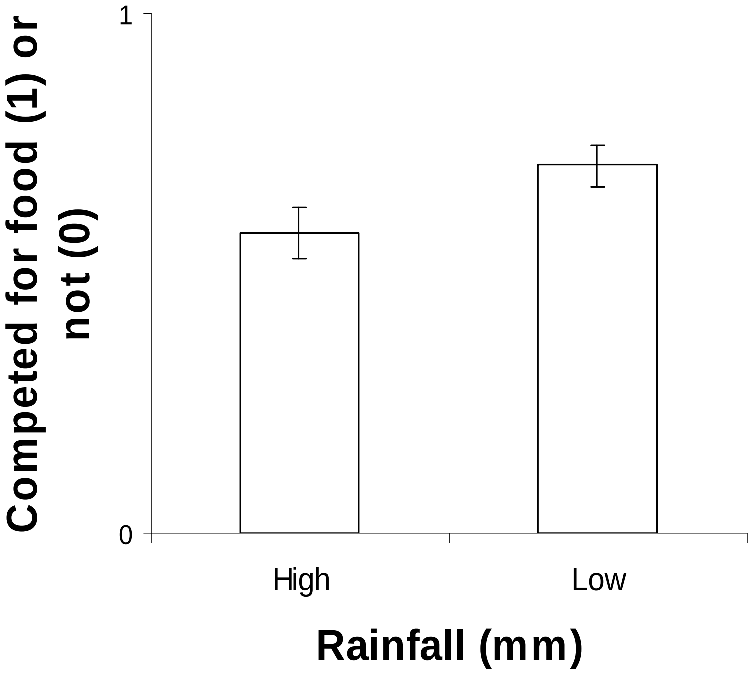
(b)



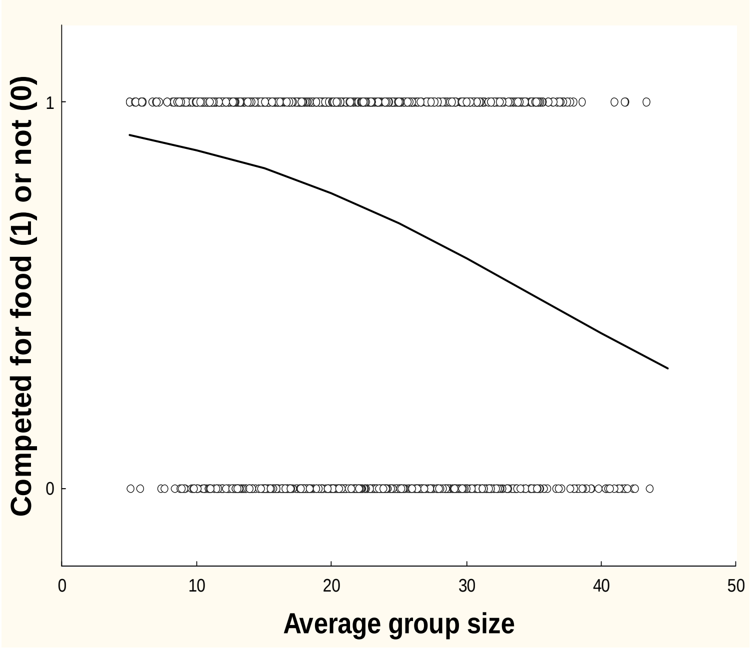
(c)


Competed for food (1) or not (0)
1
0
400
500
600
700
800
900
1000
Average morning weight (g)

(d)


Competed for food (1) or not (0)
1
0
High
Low
Rainfall (mm)

(e)


Competed for food (1) or not (0)
1
0
0
10
20
30
40
50
Average group size

(f)

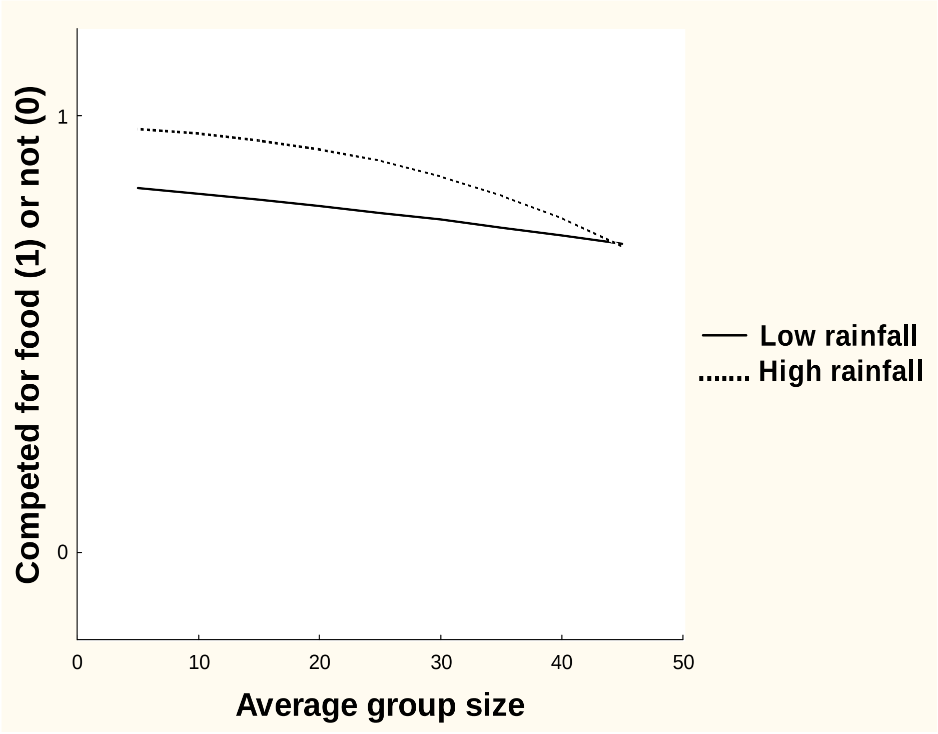

Competed for food (1) or not (0)
1
0
0
10
20
30
40
50
Average group size
—— Low rainfall
.... High rainfall

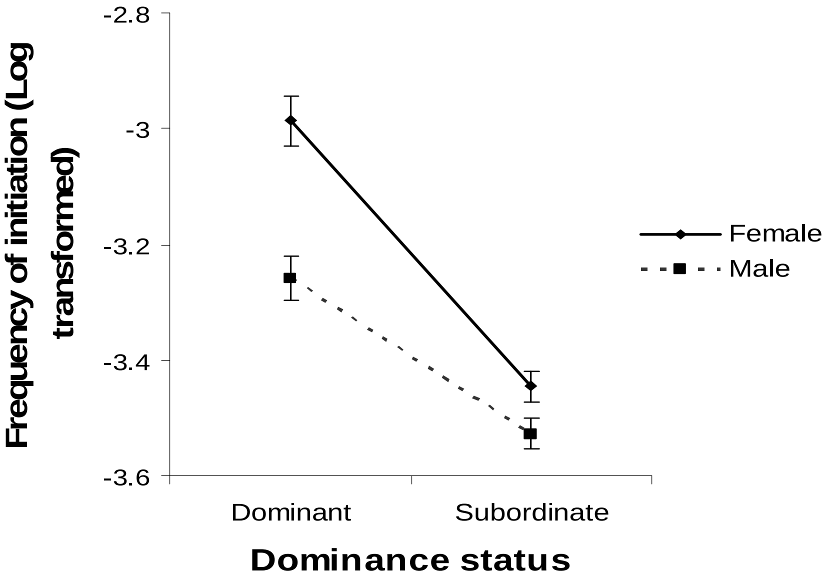
Table 2.3. LMM (with an identity link function) of the terms affecting how frequently individuals initiate competition for food.

Full model		**Wald statistic (χ^2)**	**d.f**	***P***
Dominance status		147.42	1	<0.001
Group size		32.29	1	<0.001
Sex		24.27	1	<0.001
Group size * rainfall		11.89	1	<0.001
Dominance status * sex		11.45	1	<0.001
Rainfall (high, low)		5.41	1	0.020
Weight (g)		2.95	1	0.086
Minimal model		**Effect**	**S.E.**	
Constant		-3.01	0.045	
Dominance Status	Dom	0.00	0.031	
	Sub	-0.46	0.023	
Sex	Female	0.00	0.029	
	Male	-0.27	0.027	
Group size * rainfall		See Fig. 2.3.b		
Dominance status * sex		See Fig. 2.3.a		
Rainfall	High	0.00	0.027	
	Low	0.05	0.024	
Group size		-0.02	0.01	

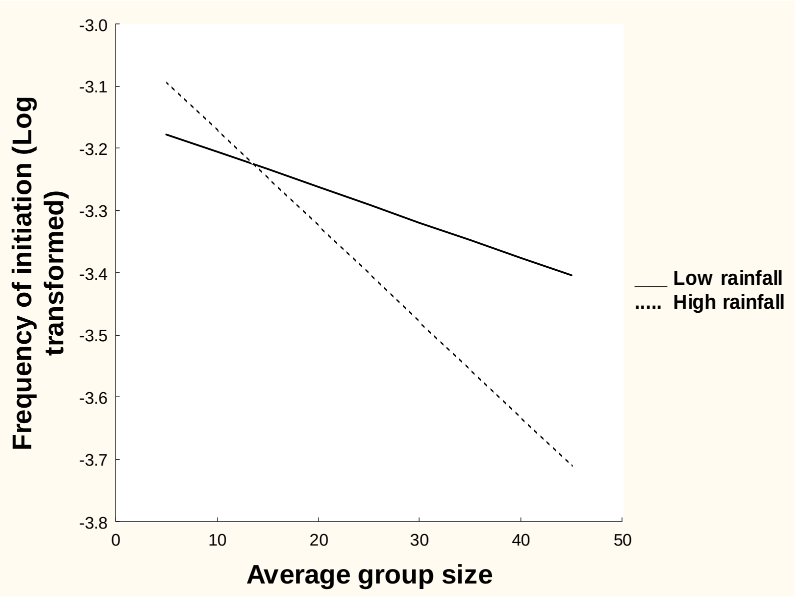
Group (component±SE=0.005±0.003), and initiator (0.02±0.005) were included as random terms in the model.

Fig. 2.3. The affect of (a) dominance status for males and females and (b) group size when rainfall is high or low, on how frequently individuals initiate competition for food. All graphs show predicted means and standard errors, or lines of best fit predicted from a LMM controlling for the effects of significant terms and random terms listed in Table 2.3.

(a)



(b)



2.4 DISCUSSION

In meerkats, the owner of a food item typically wins competition for food. Owners were more frequently successful in defending their food during competition for food irrespective of the dominance status or sex of the individual initiating competition. Meerkats feed on widely distributed food items of comparatively low value (Doolan & Macdonald 1996a). Consequently there is little opportunity for any group member to monopolise food and group members competed infrequently. Group members may therefore respect asymmetries in ownership during competition for food as the benefits of competition are typically low whilst conflict could be costly (Maan *et al* 2001). However, it is not clear whether ownership of a food item is an uncorrelated asymmetry that group members respect in competition for food, or if it confers some advantages in competition. In meerkats, the owner of a food item has typically expended some energy in obtaining a food item as they must locate and then excavate it (Doolan and Macdonald 2006a), they may therefore have a greater benefit to keeping the food item than the benefit to an individual trying to steal it. Ownership may also be a mechanical advantage in competition (Parker 1974b, Stutt & Willmer 1998) as small food items can be more easily defended (Hamilton & Busse 1982). In support of this argument, meerkats that initiated competition for larger food items, which protrude further from the mouth and require longer handling time (Brotherton *et al* 2001; Turbe 2006), were more likely to be successful. It is possible, however, that this is a result of individuals competing more aggressively for food items of greater value. Consequently this study provides evidence that group members typically respect ownership in competition for food as predicted by game theoretical models (Maynard-Smith 1982) but it is unlikely that ownership is an entirely uncorrelated asymmetry in real contests over food. However, the owner of a food item did not invariably win competition for food and there was evidence that other asymmetries between group members affected the outcome.

Asymmetries between group members in dominance also affect the outcome of competition for food. Dominant individuals were more likely to be successful in competition for food than subordinates. In meerkats competition for the opportunity to breed has resulted in a despotic dominance hierarchy where a dominant male and female monopolise reproduction (Clutton-Brock 1998; Clutton-Brock *et al* 2001b) and suppress subordinate breeding through aggression (Young *et al* 2006; Kutsukake & Clutton-Brock *In press*). Consequently there is an established dominance hierarchy and dominant individuals are likely to have asymmetries in their fighting ability or resource holding potential (RHP) with subordinates. Subordinates might also offer little resistance in competition for food with dominants in order to avoid conflict (Kutsukake & Clutton-Brock 2006b; Kutsukake & Clutton-Brock *In press*). Dominant females were also more likely to retain a food item than dominant males in competition for food, whilst subordinate females were more likely to lose a food item than subordinate males (Fig 2.1.b). This may be a consequence of there being more intense reproductive conflict between females than males in meerkats (Clutton-Brock *et al* 2006). Therefore, dominant females may be more successful at defending their food from subordinate females, whilst subordinate females are less able to defend their food from dominant females. It is unlikely that this result was a consequence of differences in fighting ability between males and females as dominant and subordinate meerkats do not show sexual dimorphism (Sharpe 2005). Reproductive conflict may therefore have important consequences for competition for food resources in cooperatively breeding species. Future study should undertake more detailed investigation of competition for food between reproductive competitors.

It is unlikely that meerkats use competition for food as a strategy to obtain large energetic benefits as competition for food is infrequent. Though the dominant male and female competed for food more frequently than other group members, they did not forego self-foraging in order to operate a ‘scrounger’ strategy in foraging, exploiting the food resources found by ‘producers’ (Barnard & Sibley 1981). In meerkats, dominants show high aggression towards subordinates, consequently subordinates may avoid conflict with them (Huntingford & Turner 1987; Clutton-Brock 2005; Kutsukake & Clutton-Brock 2006a, b; Kutsukake & Clutton-Brock *In press*). It is therefore likely that the dominant male and female compete for food more frequently because they are more likely to be successful and may suffer lower costs in competition. Competition for the opportunity to breed in group living species may therefore have consequences for the costs of conflict over other contestable resources.

Asymmetries in the costs of reproduction to the sexes may explain patterns of competition for food by females (Trivers 1972). Females initiate competition for food more frequently than males, probably because of the high costs of reproduction to females resulting from greater nutritional investment in offspring by females than males (Williams 1966; Trivers 1972). Furthermore, the dominant female initiated competition for food more frequently than all other group members. Dominant females have the highest reproductive rate in meerkat groups and breeding is particularly costly in cooperatively breeding species (Creel & Creel 1991; Clutton-Brock *et al* 2001b). Consequently the dominant female may try to steal more food than other group members as a result of the high costs of reproduction in cooperatively breeding species. Future investigation should compare patterns of competition for female when in different breeding states. This may accurately reflect the specific costs of reproduction incurred by females during pregnancy and lactation (Oftedal & Gittleman 1989).

Restrictions on the availability of food to group members are also likely to explain some variation in the frequency with which group members compete for food. Lighter adults were more likely to compete for food, which may be because lighter individuals are typically less well-nourished and additional nutrition may increase the likelihood of survival (Neuhaus 2000). Alternatively, low weight could indicate poor foraging ability (Clutton-Brock *et al* 2001a) which might increase the benefit of other strategies to obtain food. Group members also initiated competition for food more frequently during periods of low rainfall. Rainfall has been shown to strongly correlate with meerkat prey abundance in the southern Kalahari (Doolan & Macdonald 1996a; Turbe 2006) and the benefit of a food item may be higher when rainfall is low and food is rare.

Competition for food in group-living species is predicted to increase with group size (Sirot 2000; Saj & Sicotte 2007), as food resources become depleted, but in meerkats living in a smaller group may be more costly. Meerkats in smaller groups competed for food more frequently when rainfall was low. Furthermore, whilst individuals in large groups competed for food less frequently when rainfall was high, the frequency of competition by individuals in small groups was not lower than when rainfall was high. Meerkats are cooperative breeders and there is strong evidence that the costs of cooperative behaviours, including pup care and vigilance are lower in larger groups where the work load is diffused among more individuals (Clutton-Brock *et al* 1998a, 1999a, 2001a). In addition, meerkats typically breed during periods of high rainfall (Doolan & Macdonald 1997b; Clutton-Brock *et al* 1999b), and it is at these times that meerkats undertake the most costly cooperative behaviours related to pup care (Clutton-Brock *et al* 1998a; Clutton-Brock *et al* 2001a; Russell *et al* 2003). Consequently, in cooperatively breeding species, individuals in larger groups may have reduced energetic demands as a result of lower investment per individual in cooperative behaviours, whilst individuals in small groups may suffer higher energetic costs of investment in cooperative breeding (Clutton-Brock *et al* 1998a).

In summary, this study provides some empirical support for game theoretical predictions that ownership may decide the outcome of contests in group living species (Maynard-Smith 1982). In meerkats this may be a consequence of the comparatively low benefits of competition for food as the distribution of their food does not favour frequent competition and monopolization by any group member. However, in the cooperatively breeding meerkat, large asymmetries in dominance between group members also contributed to the outcome of competition for food irrespective of ownership. This may have implications for competition for food and other resources in group living species, group members use knowledge of specific asymmetries to avoid conflict but where other large asymmetries exist between group members they may decide the outcome of competition.

The frequency of competition for food by group members indicated that competition was unlikely to provide large nutritional benefits for meerkats. However, dominant individuals stole more food, indicating that competition for reproduction may effect competition for food resources. There was evidence that individuals vary how frequently they compete for food depending upon the costs and benefits of competition. Group members competed for food when it was likely to be more beneficial to them, which indicated that they may alter their behavioural strategies in response to variation in their immediate nutritional demands. Further study should investigate the mechanisms that enable individuals to monitor their energetic state and consequently respond with adaptive behaviours.

CHAPTER 3 - *The Consequences of Costly Female Reproduction for Patterns of Competition for Food in Species with High Reproductive Skew.*

ABSTRACT

Trivers (1972) predicted that females are likely to compete for food since it is typically a significant limitation on their reproductive success. Studies have shown that competition for food may be more intense amongst females than males and that success in competition for food may increase female reproductive success. However it has not been shown that females vary the extent to which they compete for food depending upon variation in the nutritional demands of their breeding state. Furthermore, reproductive skew amongst females may influence the benefits of competition for food, and this has not been previously investigated. In this study, patterns of competition for food by females were investigated in the cooperatively breeding meerkat (*Suricata suricatta*), a species in which a dominant female monopolises reproduction whilst subordinate females rarely breed. we show that both dominant and subordinate females compete for food more than males and that they compete for food more when pregnant and lactating than when not breeding. Dominant females stole more food than subordinate females and all other group members which we hypothesise was a result of the high costs of reproduction to the dominant breeding female in a species with high reproductive skew. These results provide evidence that the benefit of competition for food to female reproduction depends upon their reproductive state and may vary markedly between individuals in species with high reproductive skew.

3.1 INTRODUCTION

Females are predicted to compete with other group members for food since food is a major limitation on reproductive success (Williams 1966; Trivers 1972). Investment in offspring is energetically costly (Oftedal & Gittleman 1989; Creel & Creel 1991), and there is extensive evidence indicating that female reproductive success increases when they are able to obtain more food (e.g. Clutton-Brock 1988, Enqvist & Sauer 2003; Hofer & East 2003), or where females are in better condition (e.g. Clutton-Brock 1991, Hodge *et al* 2008). Consequently, there is likely to be strong selection on behaviours which increase the amount of food a female can obtain. In some group-living species females compete for food, and dominant individuals typically win competition and have higher reproductive success than subordinates (Imanishi, 1960; Harcourt 1987; Borries *et al* 1991; Hofer & East 2003; Wittig & Boesch 2003). The costs of reproduction and benefits of food to offspring are likely to vary according to female reproductive state. Females may therefore vary how much they compete for food when breeding (pregnant or lactating) compared with when not breeding. Furthermore, in species with high reproductive skew females will differ in how frequently they breed which may reflected how much they compete for food.

A large proportion of cooperatively breeding species have high reproductive skew, and access to reproduction is monopolised by a small proportion of the adult population

(Vehrencamp 1983b; Emlen 1991). In such societies a dominant female in the group typically monopolises reproduction though subordinates occasionally breed (Malcolm 1979; Clutton-Brock *et al* 2001b). Reproduction is costly for females in cooperatively breeding species, particularly for the dominant breeding female as a consequence of their high reproductive rate (Creel & Creel 1991, Clutton-Brock *et al* 2001b). Breeding females, particularly the dominant female, may display behavioural adaptations which optimise reproductive success (Faulkes & Abbott 1997; O'Riain *et al* 200b; Carlson *et al* 2004; Clutton-Brock *et al* 2006). Females may therefore compete for food with other group members particularly when pregnant or lactating. Furthermore, the dominant female may steal more food than subordinate females as a result of asymmetries in the costs of reproduction. Dominant individuals are typically more likely to win in competition for food resources than subordinates (Maynard-Smith & Parker 1976; Packer & Pusey 1985; Gompper 1996; Creel & Creel 1991; Hofer & East 2003). Consequently competition for food could be a tactic used by dominant females to acquire additional nutritional resources that could increase their reproductive success (Hofer & East 2003).

This study investigates the effect of breeding state and dominance status on competition for food by females in the cooperatively breeding meerkat (*Suricata suricatta*). Meerkats live in groups of 3-50 individuals (Clutton-Brock *unpublished data*) and inhabit the semi-arid regions of Southern Africa (Skinner and Smithers 1990). Groups are composed of a dominant male and female and related subordinate adults of both sexes that delay dispersal from their natal group for 1-3 years into adulthood (O'Riain 2000; Young *et al* 2005), but may also include immigrant brothers of the dominant male (Griffin *et al* 2003). The dominant female is responsible for greater than 80% of reproduction within the group (mean 2.8 litters per year) and aggressively suppresses the reproduction of subordinate females (Clutton-Brock *et al* 2001b; Young *et al* 2006; Clutton-Brock *et al* 2006), though they do occasionally breed (mean 0.9 litters per year; Clutton-Brock *et al* 2001b). Heavier females have higher reproductive success; after dominance tenure, the weight of the dominant female is the most important factor in determining her reproductive output (Hodge *et al* 2008). Heavier females (both dominant and subordinate) are also more likely to conceive, and maternal weight is the primary determinant of litter size and pup weight at weaning (Russell *et al* 2003; Clutton-Brock *et al In press*). Studies of energetics in meerkats indicate that the costs of lactation are high (Scantlebury *et al* 2002), and females have been found to increase the amount of time that they spend foraging when pregnant and lactating (Doolan & Macdonald 1997b).

This analysis will investigate the factors that affect competition for food by females in a cooperatively breeding species with high reproductive skew. The following primary questions will be addressed; (1) does competition for food by females reflect variation in the benefits of nutritional resources depending upon breeding state (pregnant, lactating or not breeding); (2) is there evidence that dominant females steal more food than subordinate females as a result of either asymmetries in dominance status or the rate at which they breed and (3) could females, specifically the dominant female, use competition for food as a behavioural tactic to monopolize food resources.

3.2 METHODS

3.2.1 Study Population

Data were collected on a free ranging population of meerkats living on ranchland located in the Southern Kalahari desert in South Africa (26°59’ S, 21°50’ E), approximately 15km south of the Botswana border. The area experienced two distinct seasons; a hot, wet ‘summer’ from October to April and cold, dry ‘winter’ from May to September (Mills 1990, Doolan & Macdonald 1996a, Clutton-Brock *et al* 1999a). Further details of the ecological conditions and climate at the study site may be found elsewhere (Russell *et al* 2002). During the study period there were between 8 and 14 groups of meerkats comprising 150 to 300 meerkats under observation at any one time. In total over 27 groups were observed comprising 810 adult (>12 months of age) individuals. All individuals were habituated to close observation at distances of less than 2 metres while foraging. One adult individual in each group was fitted with a radiocollar and the groups could therefore be easily located. Individual meerkats were instantly recognisable by unique dye marks on their fur and a unique transponder chip was inserted under the skin at the base of the neck of all individuals when they were 20 to 30 days of age to ensure a permanent record of identity. All groups in the population were visited at least every 3 days enabling the accurate collection of life history information for all individuals in the population (e.g. births, deaths, dispersal etc) allowing accurate records of group composition to be calculated for any given day. Consequently the age of 95% of the population was known to within 3 days; for the purposes of this study all analyses were restricted to adult individuals. The breeding state of all individuals was established by inspecting all group members on each visit to a group. Pregnancy was recognizable from 40 days until birth at 70 days gestation (Doolan &Macdonald 1997b; Clutton-Brock *et al.* 2001a); during pregnancy there was extensive swelling of the abdomen and weight gain, followed by large decrease in size and weight at birth. Lactation was determined by observing pups suckling and visual inspection of female meerkats nipples to check whether they were producing milk.

The weight of each meerkat could be obtained without capture by placing a small egg reward (<1g) on an electronic scale which the meerkat then obtained by climbing onto the scale. Weights were collected at groups during the morning before the group had begun foraging (morning weight) and at lunch following a prolonged foraging period of no less than 2 hours (lunch weight). The rate of morning weight gain could then be calculated (lunch weight – morning weight / foraging time). Rainfall at the study site was measured daily; rainfall strongly correlates with food abundance in the southern Kalahari (Seely & Louw 1980; Pianka 1986; Doolan and Macdonald 1996a; Barnard 2000; Turbe 2006). Consequently the average daily rainfall (mean rainfall per day) over an observation period or the total rainfall over a three month period were fitted in analyses to control for food availability.

3.2.2 Data Collection

Behavioural observations of each meerkat group were undertaken during the morning for approximately three hours and in the evening for approximately 1.5 hours, three days each week from May 1998 to May 2007. Behavioural data were collected *Ad libitum*

(Altmann 1974) and recorded on hand held Psion® data recorders. Competition for food is defined as a dyadic contest 'event' between adult individuals over a single food item, where an 'initiator' attempted to take a food item from an 'owner'. Initiation was described as approaching a foraging individual or individual with a food item to a distance of <50cm whilst looking at the owner's hole or food item and not foraging or undertaking any other behaviour. The initiator's subsequent level of aggression toward the owner was classed either as 'no contact' where it approached the owner but did not make contact, or as 'contact' when it made contact with the owner, either by pushing against them to try and obtain the hole or food item, or by physically attacking and biting them. The outcome of competition for a food item was recorded as either the initiator 'winning' or 'losing' competition with an owner for a hole/food item. The initiator was classed as winning when it took part or all of a food item or hole from the original owner and was otherwise classed as losing. Food items were also classified by size as either; 'hole', where an initiator competed for another group members excavation in progress prior to food being found; 'small', requiring between 1 and 15 chews to consume with less than 50% of the food item protruding from the mouth; or 'large', requiring >15 chews to consume and with greater than 50% of the food item protruding from the mouth.

To investigate what factors influence how frequently individual meerkats tried to steal food items and how successful they were in doing so, a single measure of each individuals 'frequency of initiation' (total number of observed initiations divided by total observation time) and 'success in competition for food' (total number of 'wins' by an initiator divided by total number of initiations) was calculated for each summer (October to April) and winter (May to September) 'observation period' throughout the study. Whenever the state of the individual changed during a summer or winter season separate measures of frequency of initiation, and success in competition were calculated, resulting in separate observation periods corresponding to the time an individual spent in each different state during a season. Individuals could change with respect to breeding state (pregnant, lactating, not breeding), dominance status (dominant, subordinate), or immigrant status (immigrant or subordinate). For the purpose of this study immigrant subordinates and dominant males in their natal groups were excluded from all analyses.

In addition, where the total observation time during an observation period was less than 10 hours, the period was excluded from all analyses. Each individuals average age (mean number of days), average morning weight (g), (mean, excluding calculations based on less than 5 morning weights), and average morning rate of weight gain (g), (mean, excluding calculations based on less than 5 rates of weight gain), were calculated for each observation period. To control for any effects of group size, average group size during an observation period (mean number of foraging individuals >3 months of age) was fitted as a variable in all analyses. Average daily rainfall during observation period (mm) was also included as a potential indicator of food availability.

3.2.3 Experimental data collection

It was difficult to obtain observational data of competition for food between specific individuals because of the low frequency of competition for food as well as the wide distribution of foraging group members (Chapter 2; Doolan & Macdonald 1996a). In order to compare competition between specific classes of individual (controlling for dominance status, age, sex and breeding state) under standardised conditions, food competition events were experimentally induced. This was achieved by presenting live scorpions to individuals in the presence of another specified individual.

Presentations were undertaken on 13 different groups from July 2006 to March 2007. All experiments involved the presentation of a live cape burrowing scorpion (Opistophthalamus Spp.) to an 'owner' individual in the presence (less than 2 meters) of an 'initiator' individual. However, in meerkat groups two specified individuals rarely forage within 2 meters of each other. Therefore a technique for manipulating where and when a scorpion was presented to an individual was developed. The last segment of the scorpion's tail was tied to a one meter length of cotton thread using pliers, and the other end was tied in a loop. The loop was passed over a nail attached to the end of a 1.8 metre stiff pole The observer could then attract the attention of the intended owner of the scorpion which was dangled in front of them, and then lead them to within 2 meters of the intended initiator whereupon the pole could be twisted to release the loop and deposit the scorpion on the ground where the owner obtained it. A digital video camera was used to record the owner obtaining the scorpion and the response of the initiator. The recording was terminated once the scorpion had been consumed. Presentations were only undertaken when >50% of the group was foraging, including the ‘initiator’. Foraging was defined as walking slowly, looking at the ground and scratching at or excavating the substrate. Video recordings were subsequently analyzed using Microsoft Windows Media player® and the initiator was scored for whether it stole the scorpion from the owner. The initiator was classified as having successfully stolen the scorpion if it took all or part of the scorpion from the owner and was otherwise classified as unsuccessful.

Experiments required the presentation of a scorpion to different dyads of meerkats on a given day at a given group and were repeated at other groups as and when the life history state of the intended competitors was appropriate. All experiments were undertaken during the first three hours of foraging in the morning. Order of dyad presentation was randomised, ensuring that there was no bias caused by satiation resulting from variation in foraging time prior to presentation. Scorpions were weighed using an electronic balance to control for size prior to presentation. In order to control for food availability, the total rainfall during the previous three months was recorded. Individuals were categorised by age and sex in all presentation pairs and the average morning weight of individuals over the previous two weeks and age on the day of presentation were also recorded.

All research protocols were approved by the University of Pretoria Ethics committee and conform to the Association for the Study of Animal Behaviour guidelines for the use of animals in research.

3.2.4 Statistical Analysis

All statistical analyses were conducted using Genstat 9.1 (Lawes Agricultural Trust, Rothamsted, Harpenden, UK). Where multivariate analyses involved repeated sampling of groups or individuals, General Linear Mixed Models (LMMs) and Generalised Linear Mixed Models (GLMMs) were used. These are similar to General and Generalised Linear

Models, but allow both fixed and random terms to be included. In all mixed models, variance components were estimated using the Restricted Maximum Likelihood (REML) method, and random terms were retained in the model unless the variance component was found to be zero. Where terms correlated (e.g. age and weight), the inclusion of both in the model could lead to spurious measures of significance (Grafen & Hails 2002; Quinn & Keough 2002). Consequently the term that had a lesser effect was excluded from analysis. In each model, all potential explanatory terms were entered together and then dropped sequentially until only those terms that explained significant variation remained. Repeating the analysis by successive inclusion of significant terms to build a minimal model using the additive method yielded an identical final model in all cases. Each dropped term was then put back into the minimal model to obtain their level of non-significance and to check that significant terms had not been wrongly excluded. All two-way interactions were tested, but were only presented if found to explain significant variation. All statistical tests were two-tailed. Unless otherwise stated, means are quoted ± 1 SE. Where data differed significantly from normality (based on the Anderson-Darling test for normality), data were transformed to attain normality or non-parametric statistics were used.

3.2.5 Factors that affect competition for food by males and females

It was previously found that females compete for food more frequently than males and dominant females compete for food more frequently than all other group members (Chapter 2; 2.3.2). To further investigate what aspects of an individual affect how successful they are in competition for food, a GLMM was used to assess what factors affect the likelihood that the initiator of competition for food is be successful in competition for food. Data were available for the success in competition for food by dominant and subordinate individuals of both sexes excluding observation periods when females were pregnant or lactating. This resulted in a data set of 1115 observation periods on 525 individuals at 23 different groups. The number of competitions initiated and won by an individual was set as the numerator and the number of competitions initiated by the individual was set as the denominator in a binomial GLMM. The following factors and variables were included as possible explanatory terms: sex, dominance status and average weight of initiator (g). The average group size and rainfall (factorised as high or low around the mean average rainfall for an observation period) were also included to control for any effect they may have. Repeated measures of group and individual were included in the model as random terms.

3.2.6 Effects of female breeding status on competition for food

To investigate whether patterns of competition for food by females change with their breeding state, analyses were undertaken to assess the factors that affect how frequently females compete for food, how frequently females are successful in competition for food, and how aggressive females were in competition for food.

In the first analysis a LMM was used to assess what factors affect how frequently females initiated competition for food. Data were available for the frequency of initiation by dominant and subordinate females that had competed at least once during an observation period, incorporating 888 observation periods on 285 individuals at 22 different groups. Frequency of initiation was logarithmically transformed and set as the response term in a LMM. The following factors and variables were included as possible explanatory terms: dominance status, average weight (g) and breeding state of initiator. The average group size and rainfall (factorised as high or low around the mean average rainfall for an observation period) were also included to control for any effect they may have. Repeated measures of group and individual were included in the model as random terms. Residuals from the model were normally distributed.

A GLMM was then used to assess what factors affect the likelihood that females initiating competition for food will be successful. Data were available for the success in competition for food by dominant and subordinate adult females, incorporating 888 observation periods on 285 individuals at 22 different groups. The number of competitions initiated and won by a female was set as the nominator and the number of competitions initiated by the female was set as the denominator in a binomial GLMM. The factors and random terms were identical to those in the model outlined above.

Finally, a GLMM was used to assess what factors affect how aggressive females were in competition for food they initiated. Data were collected from competition for food events initiated by dominant and subordinate females with subordinate males and females that were not breeding, incorporating 1899 competitions for food items. Whether a female contacted (1) or did not contact (0) an individual when initiating competition for food, was set as the binomial response term in a GLMM with the binomial denominator set at 1. The following factors and variables were included as possible explanatory terms: dominance status, breeding state, weight of initiating female on day (g) and sex of the owner of the food item. The group size on day, food item size (hole, small, large) and total rainfall in the previous three months (mm) were also included to control for any effect they may have. Repeated measures of group, individual and owner were included in the model as random terms.

Experimental Approach

To investigate whether females steal food more frequently when breeding than not breeding, presentations of scorpions to individuals in the presence of a pregnant or non pregnant female were undertaken. Separate presentation experiments were conducted on dominant and subordinate females as their pregnancies were not synchronized. In addition, presentations to three different categories of individual (old female, young female and old male) were undertaken in the experiments involving the dominant female to address questions addressed in Chapter 4 (4.3.1).

Dominant female

When the dominant female of a group was not pregnant or lactating, the eldest subordinate non-breeding natal female (mean age, 823 days), a young adult non-breeding natal female (mean age, 454 days) and the eldest natal male (mean age, 643 days) in a group were presented with a scorpion in the presence of the dominant female. These individuals were categorised as old female, young female and old male. Presentations were repeated to the same individuals when the dominant female of the group was pregnant (45 – 65 days into gestation), though it was not possible to pair the experiment where the dominant female of a group never became pregnant, lost dominance or was lost to predation during the study period. In total 69 presentations were made in the presence of the dominant female, at 13 groups when the dominant female was not pregnant, and 10 groups when the dominant female was pregnant. Whether the dominant female successfully stole the scorpion (1) or not (0), was included as the binomial response term in a GLMM with the binomial denominator set at 1. Breeding state of the dominant female (pregnant, not pregnant) and category of individual presented with the scorpion (old female, young female, old male) were included as the explanatory factors. Size of scorpion presented (small or large factorised around the mean weight), rainfall (high or low factorised around the mean total rainfall in the previous three months) and average morning weight (grams; over the previous two weeks) of individual presented with scorpion. Repeated measures of group, dominant female identity and identity of individual presented with the scorpion were included in the model

Subordinate females

To investigate whether subordinate females steal food more frequently when breeding than not breeding, we also made presentations of scorpions to an individual in the presence of a pregnant or non-pregnant subordinate female. When an adult subordinate female of a group (over 24 months in age) was pregnant, a young subordinate non breeding natal female (9 months to 24 months of age) was presented with a scorpion in the presence of the pregnant subordinate female (45 – 65 days into gestation). When the same subordinate female was no longer pregnant the presentation was repeated using the same dyad. In total 16 presentations were made at 8 groups, to the same 8 combinations of individuals. Scorpion size was standardised for all presentations and the period between presentations to the same pair of individuals was never greater than three months. A Fishers exact test was used to compare the number of times the subordinate female was successful in stealing the scorpion and the number of times that they were unsuccessful, when the subordinate female was pregnant or not pregnant.

3.3 RESULTS

3.3.1 *Factors that affect competition for food by males and females*

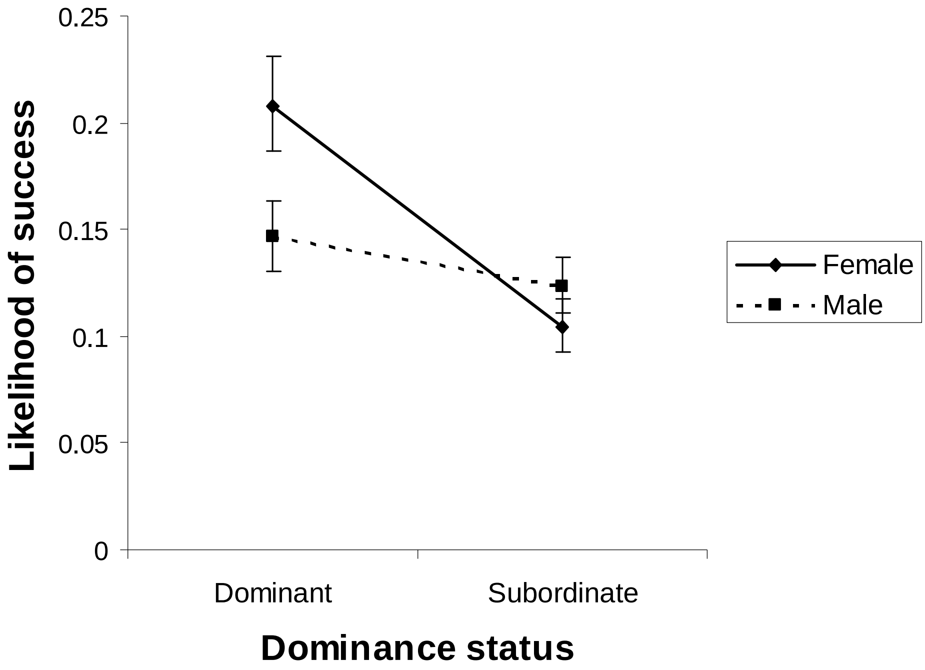
Dominant females successfully steal food items they initiate competition for on 25.99% ±31.63 (mean, S.D.) of occasions, dominant males on 18.81% ±15.59 (mean, S.D.) of occasions, subordinate females on 10.20% ±22.27 (mean, S.D.) of occasions and subordinate males on 10.24% ±21.96 (mean, S.D.) of occasions. Dominants were more likely to be successful in competition for food than subordinates, but this effect was driven primarily by dominant females, who successfully stole food at a higher rate than all other group members (GLMM: $\chi^2 = 11.29$, $P = 0.002$; Table 3.1; Fig. 3.1). Although dominant males successfully stole food more frequently than subordinates, this effect was not significant.

Table 3.1. GLMM (with a binomial distribution and a logit link function) of the terms affecting the frequency of success in competition for food by individuals.

Full model		**Wald statistic (χ^{2})**	**d.f**	***P***
Dominance status (dominant, subordinate		59.48	1	<0.001
Dominance status * sex		11.29	1	0.002
Weight (g)		9.35	1	0.002
Rainfall (high, low)		1.87	1	0.172
Group size		1.44	1	0.230
Sex		0.12	1	0.729
Minimal model		**Effect**	**S.E.**	
Constant		-1.34	0.13	
Dominance Status	Dom	0	0.11	
	Sub	-0.81	0.11	
Dominance status * sex		See Fig. 3.1		
Weight		0.002	0.0007	

Group (component±SE=0.09±0.05), and initiator (0.06±0.05) were included as random terms in the model.

Figure 3.1. The affect of dominance status and sex on the likelihood that an individual initiating competition for food will be successful. The graph shows predicted means and standard errors from a GLMM controlling for the effects of significant terms and random terms listed in Table 3.1.



3.3.2 *Effects of female breeding status on competition for food*

Direct comparison of dominant and subordinate females while controlling for the significant negative effects of group size and its interaction with rainfall shows that dominant females compete for food more frequently than subordinate females (LMM: χ^2 = 95.41, *P* = <0.001; Table 3.2; Fig. 3.2.a). When females were pregnant or lactating they initiated competition for food more frequently than when they were not breeding (LMM: χ^2 = 78.74, *P* = <0.001; Table 3.2; Fig. 3.2.b), but this effect varied according to dominance status. When subordinate females were pregnant or lactating they initiated competition for food more frequently than when not breeding, whilst dominant females only initiated competition more frequently when lactating compared with when they were not breeding (LMM interaction term: χ^2 = 7.60, *P* = 0.022; Table 3.2; Fig. 3.2.c).

Dominant females were more likely to be successful than subordinate females in competition for food they initiated, (GLMM: χ^2 = 20.98, *P* = <0.001; Table 3.3; Fig. 3.3.a), while controlling for the significant negative effects of weight and the interaction of weight and rainfall (Fig. 3.3.c). Both dominant and subordinate females were more frequently successful in competition for food when lactating than when pregnant or not breeding (GLMM: χ^2 = 19.17, *P* = <0.001; Table 3.3; Fig. 3.3.b).

Dominant females initiated contact aggression when competing for food significantly more frequently than subordinate females, (while controlling for the significant positive effects of food item size and negative effects of group size; GLMM: χ^2_1 = 18.03, *P* = <0.001; Table 3.4; Fig. 3.4). However, neither dominant females nor subordinate females were more likely to initiate contact aggression in competition for food when pregnant or lactating than when not breeding (GLMM: χ^2_2 = 1.99, *P* = 0.370; Table 3.4).

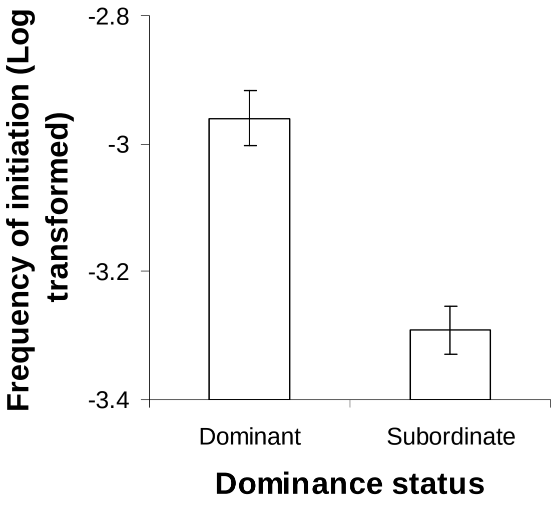
Table 3.2. LMM (with an identity link function) of the terms affecting how frequently females initiate competition for food.

Full model		**Wald statistic (χ^{2})**	**d.f**	***P***
Dominance status (dominant, subordinate)		95.41	1	<0.001
Breeding state (lactating, pregnant, non breeding)		78.74	2	<0.001
Group size		30.16	1	<0.001
Group size * rainfall		10.37	1	<0.001
Dominance status * breeding state		7.60	2	0.022
Rainfall (high, low)		0.43	1	0.51
Weight (g)		0.21	1	0.64
Minimal model		**Effect**	**S.E.**	
Constant		-2.91	0.05	
Dominance Status	Dom	0	0.04	
	Sub	-0.30	0.04	
Breeding state	Lactating	0	0.04	
	Pregnant	-0.08	0.04	
	Non Breed	-0.11	0.04	
Group size		-0.01	0.003	
Group size * rainfall		See Fig. 3.2.d		
Dominance status * breeding state		See Fig. 3.2.c		

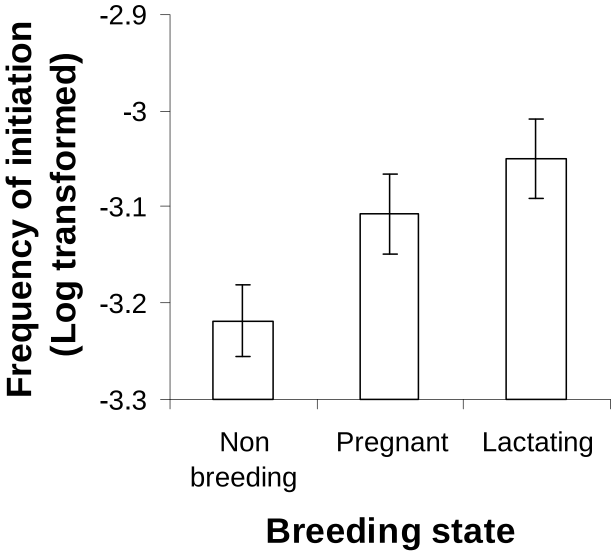
Group (component±SE=0.01±0.006), and initiator (0.02±0.005) were included as random terms in the model.

Figure 3.2. The affect of (a) dominance status (b) breeding state (c) breeding state when females are dominant or subordinate and (d) group size when rainfall is high or low, on how frequently females initiate competition for food. All graphs show predicted means and standard errors or lines of best fit predicted from a LMM controlling for the effects of significant terms and random terms listed in Table 3.2.

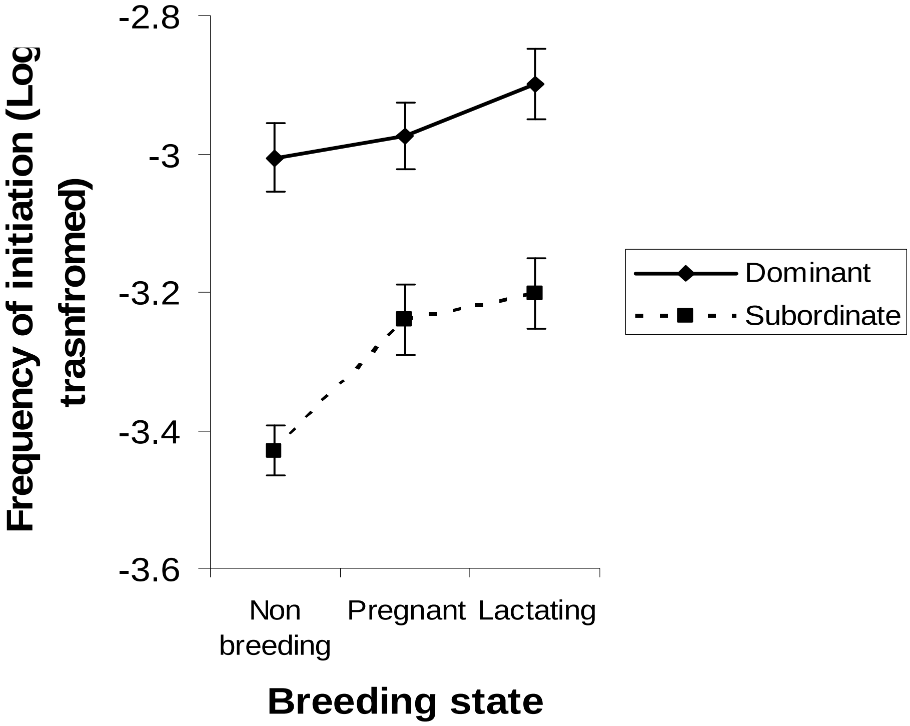
(a)



(b)



(c)


-2.8
-3
-3.2
-3.4
-3.6
Frequency of initiation (Log trasnfromed)
Non breeding
Pregnant
Lactating
Breeding state
Dominant
Subordinate

(d)

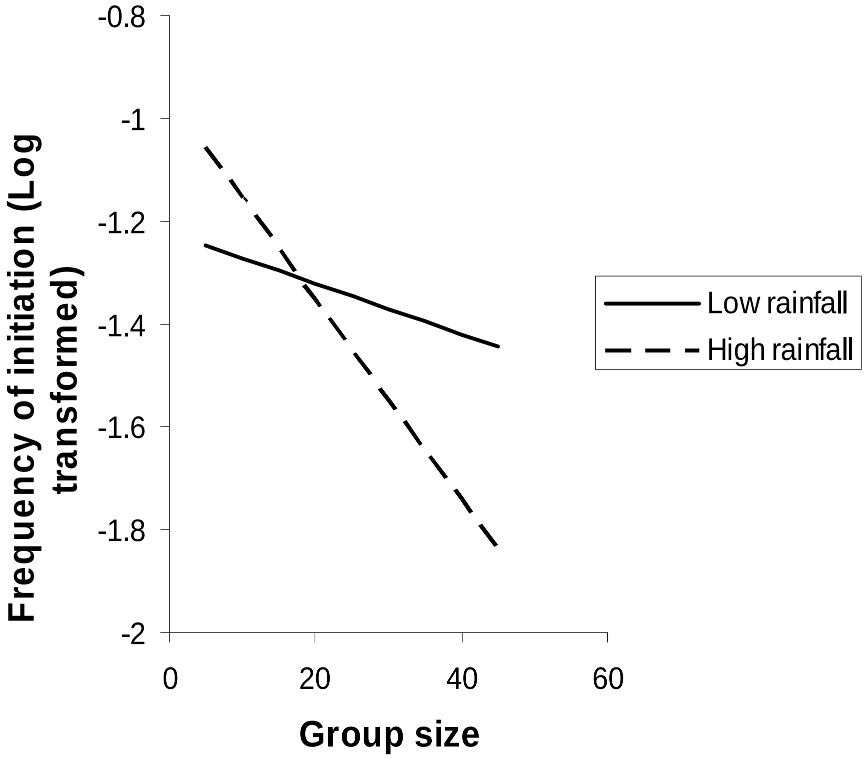

-0.8
-1
-1.2
-1.4
-1.6
-1.8
-2
0
20
40
60
Frequency of initiation (Log transformed)
Group size
Low rainfall
High rainfall

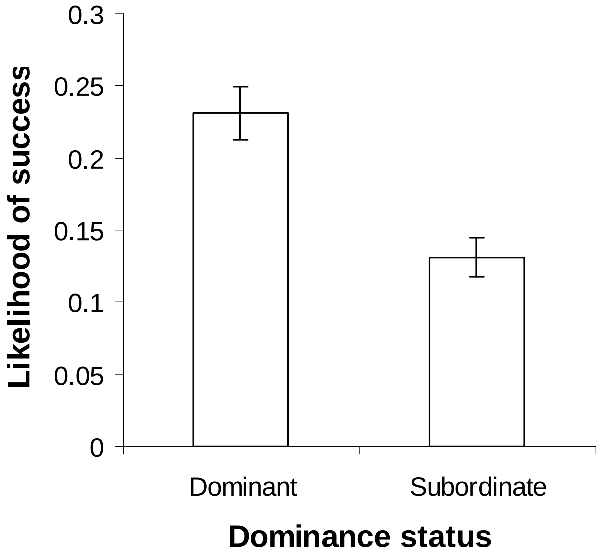
Table 3.3. GLMM (with a binomial distribution and a logit link function) of the terms affecting how frequently females are successful in competition for food

Full model		**Wald statistic (χ^2)**	**d.f**	***P***
Dominance status (dominant, subordinate)		20.98	1	<0.001
Breeding state (lactating, pregnant, non breeding)		19.17	2	<0.001
Weight (g)		7.37	1	0.007
Weight * Rain		7.01	1	0.008
Rain (high, low)		3.21	1	0.073
Group size		0.12	1	0.733
Minimal model		**Effect**	**S.E.**	
Constant		-0.10	0.13	
Dominance Status (dominant, subordinate)	Dom	0	0.10	
	Sub	-0.69	0.12	
Breeding state (lactating, pregnant, non breeding)	Lactating	0	0.11	
	Pregnant	-0.47	0.10	
	Non Breed	-0.39	0.10	
Weight (g)		0.0007	0.0008	
Weight * Rain		See Fig. 3.3.c		

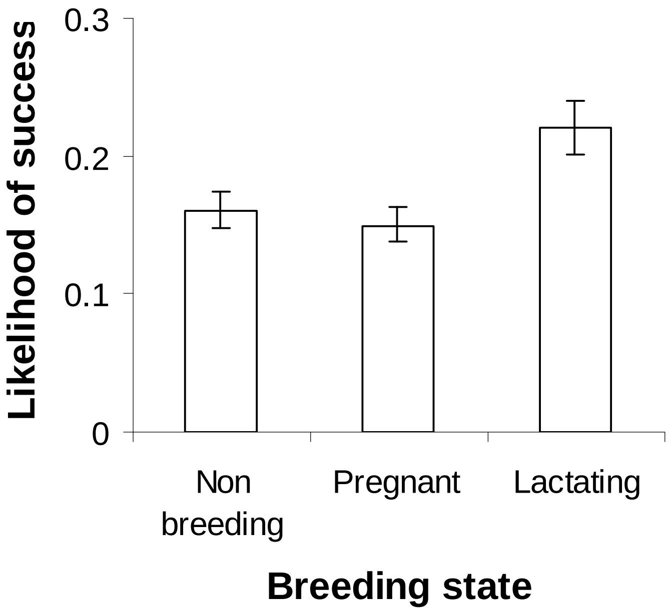
Group (component±SE=0.008±0.03), and initiator (0.18±0.07) were included as random terms in the model.

Figure 3.3. The affect of (a) dominance status (b) breeding state and (c) weight of female when rainfall is low or high on how frequently females are successful in competition for food. All graphs show predicted means and standard errors or lines of best fit predicted from a GLMM controlling for the effects of significant terms and random terms listed in Table 3.3.

(a)



(b)



(c)

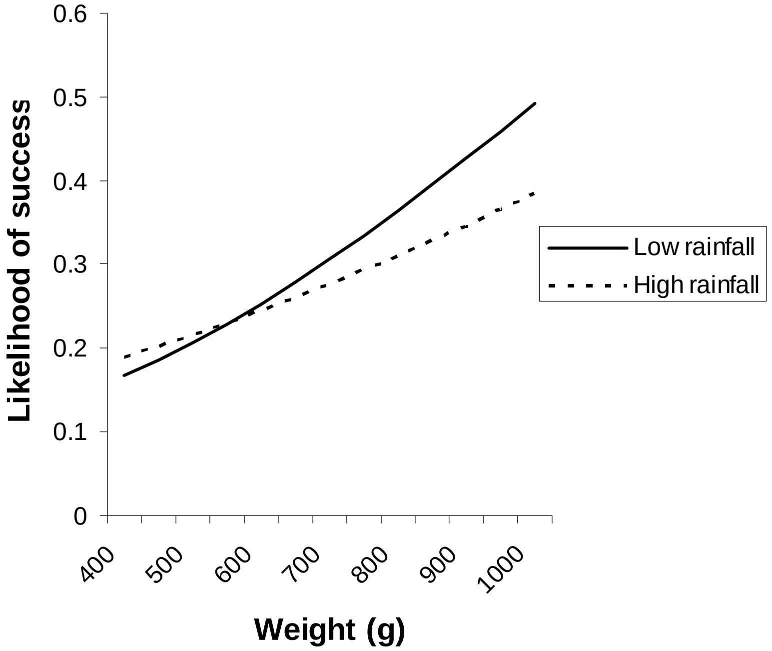
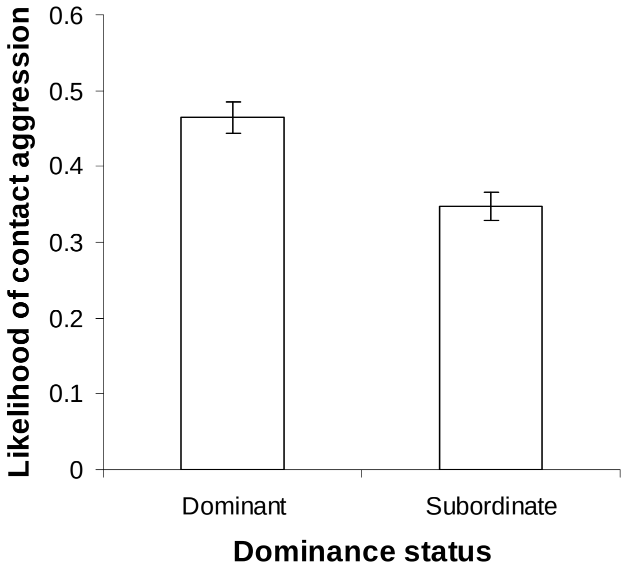


Table 3.4. GLMM (with a binomial distribution and a logit link function) of the terms affecting how aggressive females are when competing for food

Full model		**Wald statistic (χ^2)**	**d.f**	***P***
Group Size		19.77	1	<0.001
Dominance status (dominant, subordinate)		18.03	1	<0.001
Food Size (hole, small, large)		7.35	2	0.03
Breeding state (lactating, pregnant, non breeding)		1.99	2	0.37
Weight (g)		0.63	1	0.43
Rain (high, low)		0	1	0.99
Minimal model		**Effect**	**S.E.**	
Constant		-0.14	0.12	
Group size		0.03	0.007	
Dominance Status	Dom	0	0.08	
	Sub	-0.49	0.08	
Food size	Hole	0	0.09	
	Small	-0.17	0.10	
	Large	0.15	0.08	

Initiator (component±SE=0.03±0.04), and owner (0.08±0.06) were included as random terms in the model.

Figure 3.4. The affect of dominance status on how likely a female is to initiate contact aggression in competition for food. All graphs show predicted means and standard errors from a GLMM controlling for the effects of significant terms and random terms listed in Table 3.4.



Experimental Approach

Dominant females were significantly more likely to steal a presented scorpion from another individual when pregnant than when not pregnant (GLMM: $\chi^2_1 = 6.52$, $P = 0.011$; Table 3.5; Fig. 3.5) while controlling for the significant effect of scorpion size and category of individual presented with the scorpion (discussed in Chapter 4; 4.3.1). Dominant females stole the scorpion from the individual whom it was presented to on 7 of 45 occasions (15.56%) when the dominant female was not pregnant, and on 13 of 31 occasions (41.94%) when pregnant. Conversely subordinate females were not more likely to steal a scorpion when pregnant than when not pregnant (Fishers exact test: $P = 0.999$).

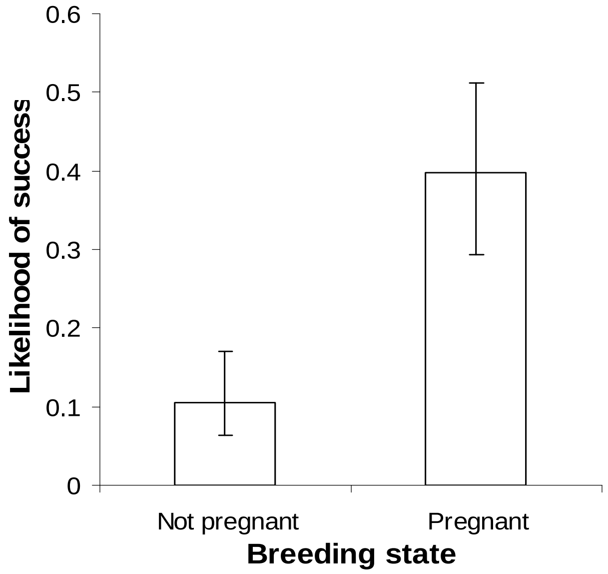
Table 3.5. GLMM (with a binomial distribution and a logit link function) of the terms affecting whether a dominant female successfully stole a scorpion from another individual

Full model		**Wald statistic (χ^2)**	**d.f**	***P***
Competitor category (old female, young female, old male)		9.14	2	0.010
Breeding state of dominant female (not pregnant, pregnant)		6.52	1	0.011
Scorpion size (small, large)		4.47	1	0.035
Rainfall (high, low)		1.77	1	0.184
Weight of food owner (g)		0.12	1	0.730
Minimal model		**Effect**	**S.E.**	
Constant		-2.744	0.9717	
Competitor	Old male	0	0.835	
	Young female	1.170	0.494	
	Old female	2.831	0.637	
Breeding state of dominant female	Non pregnant	0	0.55	
	Pregnant	1.721	0.467	
Scorpion Size	Large	0	0.498	
	Small	-1.4594	0.533	

Presence (component±SE=0.006±0.81), and Presented (0.58±1.33) were included as random terms in the model.

Figure 3.5. The affect of breeding state on the likelihood that the dominant female stole a scorpion form another individual. All graphs show predicted means and standard errors from a GLMM controlling for the effects of significant terms and random terms listed in Table 3.5.

(a)



3.4 DISCUSSION

In the cooperatively breeding meerkat, females compete for food more than males and we have previously shown that females initiate competition for food more frequently than males (Chapter 2; Table 2.3.2). Further investigation shows that dominant females are more successful in competition for food than dominant males. Females initiate competition for food more frequently when breeding (pregnant and lactating) than when not breeding. Females were also more likely to be successful in competition for food when lactating, and experimental presentation of food demonstrated that dominant females successfully stole food items more frequently when they were pregnant than when not pregnant. These results indicate that females compete for food because of the benefit of food for female reproduction (Williams 1966), particularly when facing the immediate costs of breeding (Clutton-Brock 1998, Enqvist & Sauer 2003; Hofer & East 2003). It is likely that females are more successful in competition for food when breeding as a result of asymmetries in the value of the resource to breeding females and other group members (Maynard-Smith & Parker 1976; Krebs 1982). Results also support the conclusion that lactation is the most energetically costly period of reproduction in females (Oftedal & Gittleman 1989; Creel & Creel 1991; Scantlebury *et al* 2002). When lactating, females initiated competition for food more frequently, and were more likely to be successful in competition, than in any other breeding state. This indicates that females compete for food with group members as a result of the high costs of reproduction in females and the potential benefits of food to their reproductive success. Furthermore, they vary how much they compete for food according to the immediate energetic demands of their breeding state.

In meerkats, dominant breeding females may steal more food than other group members as a result of asymmetries in dominance and the increased energetic demands of reproduction in species with high reproductive skew (Creel & Creel 1991; Clutton-Brock *et al* 2001b). Comparison of competition for food by dominant and subordinate females in different breeding states shows that dominant females initiated competition for food more frequently and were more likely to be successful in competition than subordinate females. Furthermore, they were more aggressive in competition for food than subordinate females. These results were supported by experimental scorpion presentations, with dominant and subordinate females differing widely in their success in attempts to steal food from other group members. Consequently, the dominant female steals more food than subordinate females. This is likely to be a result of both asymmetries in dominance status between the dominant female and other group members. Asymmetries in dominance status enable dominant male and female meerkats to win competition for food more frequently than subordinates, and the reduced costs of conflict may result in them competing more frequently (discussed in Chapter 2). However, dominant females were previously found to initiate competition for food more frequently than dominant males (Chapter 2), and results from this study show that they are more likely to be successful when they initiate competition for food than dominant males. Consequently, asymmetries in dominance status do not entirely explain why the dominant females initiate competition for food more frequently and are more successful than any other group member, since dominant males and females differ in their stealing strategies. As a result of reproductive skew, dominant females can have up to four litters of pups per year whilst subordinate females rarely breed (Clutton-Brock *et al* 2001b) and breeding is particularly costly in cooperative breeders (Creel & Creel 1991). The dominant female may therefore have higher energetic requirements than other group members. Consequently asymmetries in the value of the resource to the dominant female compared with other group members may also be a factor that affects the outcome of competition for food enabling the dominant female to steal more food (Maynard-Smith & Parker 1976; Koenig 1982). In summary, dominant females may steal more food than other group members as a result of both their dominance status and the high nutritional requirements of the dominant breeding. This may have important consequences for the costs of reproduction for both dominant and subordinate females in cooperatively breeding species (Creel & Creel 1991).

It is unlikely that females, particularly the dominant female, use competition for food when breeding as a behavioural strategy to monopolise food. The number of food items obtained by an individual in competition for food, an indicator of the energetic payoff, is a product of the frequency of competition for food multiplied by the likelihood that an individual will be successful. In meerkats, opportunities to compete for food are rare, as items are typically small and widely distributed (Doolan & Macdonald 1996a). Consequently lactating dominant females competing at their highest frequency of 0.16 ±0.17 (mean, S.D.) competitions for food per hour with their greatest mean likelihood of success of 35% ±31 (mean, S.D.) would still only obtain 0.040 food items per hour. In contrast self-foraging meerkats obtain food items at least every few minutes (Clutton-Brock *unpublished* data). It is therefore likely that patterns of competition for food by female meerkats reflect the high costs of reproduction and potential benefit of food resources when breeding. Stealing food from other group members is unlikely to make a large difference to their reproductive success but may reflect the opportunity for stealing coupled with a reduced cost associated with asymmetry in dominance. However, asymmetries in dominance and reproductive output could have more significant consequences for competition for food by females in species with similar high reproductive skew but where the opportunity for competition for food is common and dominant females could monopolise food.

Patterns of competition for food by individual females reflected the immediate nutritional demands of their breeding state. The dominant female stole more food than subordinate females which is likely to be a result of asymmetries in both dominance status and the costs of reproduction resulting from high reproductive skew. Although competition for food in meerkats is unlikely to contribute significantly to their reproductive success, there is evidence from other cooperatively breeding species with high reproductive skew that nutritional requirements of breeding can have important consequences for competition for food. In the spotted hyena (*Crocuta crocuta*) for example, high costs of reproduction result in intense competition for food amongst females (Frank 1986). Dominant females are able to obtain more food resources and consequently have higher reproductive success (Hofer & East 2003). Future investigation of competition for food in cooperatively breeding species should focus on species with a despotic dominance structure where opportunities to monopolise food are common. Under these circumstances the dominant female may use competition for food as a behavioural tactic to steal food, increasing their reproductive success.

CHAPTER 4 - *The Consequences of Reproductive Conflict for Competition for Food in a Cooperatively Breeding Species.*

ABSTRACT

In some group living species, competition for limited breeding opportunities results in intense reproductive conflict. Consequently, there is strong selection for behavioural traits that increase competitive ability and may contribute to reproductive suppression. However the consequences of reproductive conflict for patterns of competition for food in group living species have not been considered previously. In this study I test the possibility that competition for food may function as a behavioural tactic for reproductive suppression in the cooperatively breeding meerkat (*Suricata suricatta*). I show that, in meerkats, the group members that are reproductively suppressed by dominant females are also those with whom dominant females are most successful against and most aggressive towards during competition for food. Competition for food by dominant females with

their competitors could therefore reinforce dominance and contribute to reproductive suppression. In comparison, patterns of competition for food by dominant males, subordinate males and subordinate females indicate no effect of reproductive conflict. This difference is likely to be a consequence of there being more intense reproductive conflict between dominant and subordinate females than exists between other group members. Evidence is therefore provided that competition for food may function as a means of reproductive suppression in species with high reproductive conflict.

4.1 INTRODUCTION

In some group-living species, competition for limited opportunities to breed can result in high reproductive skew (Vehrencamp 1983b; Emlen 1991; Clutton-Brock *et al* 2006). Under these conditions dominant individuals typically monopolise the majority of breeding and reproductively suppress subordinate group members (Keller & Reeve 1994; Creel & Macdonald 1995; Kokko & Johnstone 1999). As a consequence, reproductive conflict between some group members is intense and strong sexual selection may operate on behavioural traits that increase competitive ability (Clutton-Brock *et al* 2006). Dominant individuals use a variety of behavioural tactics for the reproductive suppression of their competitors, including infanticide (Malcolm 1979; Clutton-Brock *et al* 2001b), intervention in mating by subordinates (Nishida, 1979) and reduction of subordinate fertility through aggression (Schmidt 1988; Creel *et al* 1992; Faulkes & Abbott 1997; Young *et al* 2006). Subordinate individuals may also compete for a share of reproduction with both the dominant individuals in the group and other subordinates (Creel & Waser 1997; Griffin *et al* 2003; Clutton-Brock *et al* 2006; Hodge *et al* 2008), and they use behavioural tactics to increase the likelihood that they will reproduce (Young & Clutton-Brock 2006). Reproductive conflict is therefore important in determining the behaviour of group members. The consequences of reproductive conflict for patterns of competition for food between reproductive competitors have not previously been considered. Competition for food may reflect patterns of reproductive suppression; during competitive interactions dominant individuals may be more likely to initiate and win, and subordinate individuals may be more likely to lose or relinquish items (Kutsukake & Clutton-Brock 2006 a, b). This could result from both aggression by the dominant individual or avoidance of conflict by the subordinate. Individuals could compete for food with their reproductive competitors as a means of dominance assertion or to deprive them of nutritional resources. Either of these tactics could contribute to reproductive suppression. Consequently, competition for food could function as a tactic for reproductive suppression of subordinate females by dominant breeding females.

This study investigates the consequences of reproductive conflict for competition for food between group members in the cooperatively breeding meerkat (*Suricata suricatta*). Meerkats live in groups of 3-50 individuals (Clutton-Brock *unpublished data*) and inhabit the semi-arid regions of Southern Africa (Skinner and Smithers 1990). Groups are composed of one dominant female, one dominant male and related subordinate adults of both sexes that delay dispersal from their natal group for 1-3 years into adulthood (O'Riain 2000; Young *et al* 2005). The groups may also include subordinate immigrant brothers of the dominant male unrelated to the dominant female (Griffin *et al* 2003). There is high reproductive skew amongst both male and female group members (Griffin *et al* 2003) and individuals compete for the opportunity to breed (Clutton-Brock 2001b; Young & Clutton-Brock 2006; Young *et al* 2006). The dominant male and female are responsible for more than 80% of reproduction within the group and prevent subordinate same-sex competitors from breeding by aggressively suppressing their reproduction (Clutton-Brock *et al* 2001b; Young *et al* 2006; Clutton-Brock *et al* 2006; Kutsukake & Clutton-Brock *in press*). All adult subordinate females have the potential to breed in the group (Griffin 2003; Young *et al* 2005), and are occasionally successful in reproducing (Clutton-Brock *et al* 2001b). Older and heavier subordinate females in particular are more likely to conceive and less likely to abort pregnancies (Hodge *et al*. *In press*). Subordinate natal males are related to female group members and consequently cannot breed within their own group, but subordinate immigrant males may breed with the dominant female and sometimes with subordinate females (Griffin *et al* 2003). Unlike females, both subordinate and immigrant males may breed outside the group as they commonly prospect at other groups where they may mate with females (Griffin *et al* 2003; Young *et al* 2005).

It is likely that allowing subordinate females to breed would reduce the available resources for the dominant's own pups, as pup growth and survival decreases with a lower helper to pup ratio (Clutton-Brock *et al* 2001c). The dominant female therefore usually kills any pups born to subordinate female when she is pregnant herself (Clutton-Brock 2001b). When subordinate females are pregnant they can also commit infanticide, killing the offspring of both the dominant female and other subordinate females (Young & Clutton-Brock 2006). Dominant females show counter-tactics in reproductive suppression of subordinate female that minimize infanticide of their own offspring by reducing the likelihood that there will be any pregnant females in the group when they give birth (Young & Clutton-Brock 2006; Young *et al* 2006). The dominant female achieves this through aggression towards subordinate females and evicting them from the group during her pregnancy (Clutton-Brock *et al* 1998b; Young *et al* 2006). This induces chronic stress in subordinate females resulting in down-regulation of their reproductive state, during eviction females are also more likely to abort pregnancies and less likely to conceive (Young *et al* 2006). Older females show less reduction in fertility and are less likely to abort pregnancies (Young *et al* 2006; Hodge *et al. In press*), which may explain why they are the principle target of aggression by the dominant female and why older females as well as pregnant females are more likely to be evicted by the dominant female during her pregnancy (Kutsukake & Clutton-Brock 2006b; Young *et al* 2006). Therefore reproductive suppression by the dominant female is primarily targeted at older females, and peaks when the dominant female is herself pregnant.

Dominant males prevent subordinate immigrant males from breeding within the group by mate-guarding the dominant female during the oestrus period (Griffin *et al* 2003; Kutsukake & Clutton-Brock *In press*). They also show increased aggression towards subordinate immigrant males compared with natal males, but this is only evident in large groups (Kutsukake & Clutton-Brock *In press*). Consequently, there is some evidence of reproductive conflict between the dominant male and males in the group that are unrelated to the dominant female.

Aggressive intrasexual competition amongst natal subordinate male or female group members is infrequent (Clutton-Brock *unpublished* data), but subordinates do fight with other same sex group members from their natal group for the position of dominance when it is available, which commonly results in severe injury (Sharpe 2005; Hodge *et al* 2008). Usually the eldest individual obtains dominance, but where there is no difference in age (littermates), heavier females more frequently obtain the dominance position whilst no such relationship is found in males (Hodge *et al* 2008). Consequently, natal subordinate individuals are likely to be future reproductive competitors and in females weight is important to competitive ability (Clutton-Brock *et al* 2006; Hodge *et al* 2008).

In this study I first investigate the consequences of reproductive conflict between dominant and subordinate females for patterns of competition for food. I then consider whether competition for food may function as a behavioural tactic of dominant females for reproductive suppression. Reproductive suppression through competition for food could occur in two ways; (a) aggressive encounters could reinforce dominance assertion over competitors; and (b) it may deprive competitors of nutrition, which could increase the initiator's own competitive ability at the cost of the competitor. The consequences of reproductive conflict for patterns of competition for food by dominant males with males unrelated to the dominant female and subordinate males and females with same sex subordinates, will then be addressed. Finally, I will compare the effect of reproductive conflict on competition for food by dominant females, dominant males and subordinate natal males and females will be undertaken.

4.2 METHODS

4.2.1 *Study Population*

Data was collected on a free ranging population of meerkats living on ranchland located in the Southern Kalahari desert in South Africa (26°59' S, 21°50' E), approximately 15km south of the Botswana border. The area experienced two distinct seasons; a hot, wet 'summer' from October to April and cold, dry 'winter' from May to September (Mills 1990, Doolan & Macdonald 1996a, Clutton-Brock *et al* 1999a). Further details of the ecological conditions and climate at the study site may be found elsewhere (Russell *et al* 2002). During the study period the population comprised 8 to 14 groups of meerkats containing approximately 150 to 300 meerkats at any one time. In total over 27 groups were observed comprising 810 adult (>12 months of age) individuals. All individuals were habituated to close observation at distances of less than 2 metres while foraging. One adult individual in each group was fitted with a radiocollar and the groups could therefore be easily located. Individual meerkats were instantly recognisable by unique dye marks on their fur and a unique transponder chip was inserted under the skin at the base of the neck of all individuals when they were 20 to 30 days of age to ensure a permanent record of identity. All groups in the population were visited at least every 3 days enabling the accurate collection of life history information for all individuals in the population (e.g. births, deaths, dispersal etc) allowing accurate records of group composition to be calculated for any given day. Consequently, the age of 95% of the population was known to within 3 days. For the purposes of this study, analyses were restricted to adult individuals and adults were classified as either 'young' (12 to 30 months of age) or 'old' (>30 months of age). The breeding state of all individuals was established by inspecting all group members on each visit to a group. Pregnancy was recognizable from 40 days until birth at 70 days gestation (Doolan &Macdonald 1997; Clutton-Brock *et al.* 2001a). During pregnancy there was extensive swelling of the abdomen and weight gain, followed by large decrease in size and weight at birth. Lactation was determined by observing pups suckling and visual inspection of a female's nipples to check whether they were producing milk. The weight of each meerkat could be obtained without capture by placing a small egg reward (<1g) on an electronic scale which the meerkats would then get by climbing onto the scale. Weights were collected at groups during the morning before the group had begun foraging (morning weight) and at lunch following a prolonged foraging period of no less than 2 hours (lunch weight). The rate of morning weight gain could then be calculated (lunch weight – morning weight / foraging time). Rainfall at the study site was measured daily. Rainfall strongly correlates with food abundance in the southern Kalahari (Seely & Louw 1980; Pianka 1986; Doolan and Macdonald 1996a; Barnard 2000; Turbe 2006). Consequently the average daily rainfall (mean rainfall per day) over an observation period or the total rainfall over a three month period were fitted in analyses to control for food availability.

4.2.2 Data Collection

Behavioural observations of each meerkat group were undertaken during the morning for approximately three hours and in the evening for approximately 1.5 hours, three days each week from May 1998 to May 2007. Behavioural data were collected *Ad libitum* (Altmann 1974) and recorded on hand held Psion® data recorders. Competition for food is defined as dyadic contest 'events' between adult individuals (>12 months) over a single food item, where an 'initiator' attempted to take a food item from an 'owner'. Initiation was described as approaching a foraging individual or individual with a food item to a distance of <50cm whilst looking at the owner's hole or food item and not foraging or undertaking any other behaviour. The initiator's subsequent level of aggression toward the owner was classed either as 'no contact' where it approached the owner but did not make contact (the owner would typically growl and/or block access to the food item); or as 'contact' when it made contact with the owner either by pushing against them to try and obtain the hole or food item, or by physically attacking and biting them. The outcome of competition for a food item was recorded as either the initiator 'winning' or 'losing' competition with an owner for a hole/food item. The initiator was classed as winning when it took part or all of a food item or hole from the original owner and was otherwise classed as losing. Food items were also classified by size as either; 'hole', where an initiator competed for another group members excavation in progress prior to food being found; ‘small’, requiring between 1 and 15 chews to consume with less than 50% of the food item protruding from the mouth; or ‘large’, requiring >15 chews to consume and with greater than 50% of the food item protruding from the mouth.

To investigate the factors that influence the frequency with which individual meerkats tried to steal food items, and their success, a single measure of each individuals ‘frequency of initiation’ (total number of observed initiations divided by total observation time) and ‘success in competition for food’ (total number of ‘wins’ by an initiator divided by total number of initiations) was calculated for each summer (October to April) and winter (May to September) ‘observation period’ throughout the study. Whenever the state of the individual changed during a summer or winter season separate measures of frequency of initiation, and success in competition were calculated, resulting in separate observation periods corresponding to the time an individual spent in each different state during a season. Individuals could change with respect to breeding state (pregnant, lactating, not breeding), dominance status (dominant, subordinate), or immigrant status (immigrant or subordinate). For the purpose of this study dominant males in their natal groups were excluded from analyses. In addition, where the total observation time during an observation period was less than 10 hours, the period was excluded from any analysis. Each individual’s average age (mean number of days), average morning weight (g), (mean, excluding calculations based on less than 5 morning weights), average morning rate of weight gain (g), (mean, excluding calculations based on less than 5 rates of weight gain), were calculated for each observation period. To control for the effects of group size, average group size during an observation period (mean number of foraging individuals >3 months of age) was fitted as a variable in all analyses. Average daily rainfall during observation period (mm) was also included to control for the effect of food availability.

In order to compare the factors that influenced competition for food between different categories of individual, it was necessary to calculate the frequency of initiation and success in competition for food for a given individual when acting as an initiator with different categories of owners. For each individual, values for frequency of initiation and success in competition for food were calculated for competition with owners of differing ages (young or old adults), sexes, dominance status (dominant or subordinate) and immigration status (immigrant or natal). Owners that were either pregnant or lactating were excluded from the analysis. The frequency of initiation was also divided by the average number of individuals in the category of adult competed with during each period. This controlled for the likelihood that an individual would encounter group members from different categories and therefore have the opportunity to compete with them, where the number of individuals in each demographic category varied within the group.

4.2.3 Experimental data collection

It is difficult to obtain observational data of competition for food between specific individuals because of the low frequency of competition for food as well as the wide distribution of foraging group members (Chapter 2; Doolan & Macdonald 1996a). In order to compare competition between specific classes of individual (controlling for dominance status, age, sex and breeding state) under standardised conditions, food competition events were experimentally induced. This was achieved by presenting live scorpions to individuals in the presence of another specified individual.

The experimental procedure for presentations is presented in detail in Chapter 3 (3.2.3). Briefly, presentations were undertaken on 13 different groups from July 2006 to March 2007. All experiments involved the presentation of a live cape burrowing scorpion (Opistophthalamus Spp.) to an ‘owner’ individual in the presence (less than 2 meters) of an ‘initiator’ individual. Since individuals rarely forage within 2 meters of each other, I devised a technique to entice the owner into proximity with the initiator before releasing the scorpion food item. A digital video camera was used to record the owner obtaining the scorpion and the response of the initiator. The recording was terminated once the scorpion had been consumed. Presentations were only undertaken when >50% of the group was foraging, including the ‘initiator’. Foraging was defined as walking slowly, looking at the ground and scratching at or excavating the substrate. Video recordings were subsequently analyzed using Microsoft Windows Media player® and the initiator was scored for whether it stole the scorpion from the owner. The initiator was classified as having successfully stolen the scorpion if it took all or part of the scorpion from the owner and was otherwise classified as unsuccessful.

Experiments required the presentation of a scorpion to different dyads of meerkats on a given day at a given group and were repeated at other groups as and when the life history state of the intended competitors was appropriate. All experiments were undertaken during the first three hours of foraging in the morning. Order of dyadic presentation was randomised, ensuring that there was no bias caused by satiation resulting from variation in foraging time prior to presentation. Scorpions were weighed using an electronic balance to control for size prior to presentation. In order to control for food availability, the total rainfall during the previous three months was recorded. Individuals were categorised by age and sex in all presentation pairs and the average morning weight of individuals over the previous two weeks and age on the day of presentation were also recorded.

All research protocols were approved by the University of Pretoria Ethics committee and conform to the Association for the Study of Animal Behaviour guidelines for the use of animals in research.

4.2.4 Statistical Analysis

All statistical analyses were conducted using Genstat 9.1 (Lawes Agricultural Trust, Rothamsted, Harpenden, UK). Where multivariate analyses involved repeated sampling of groups or individuals, General Linear Mixed Models (LMMs) and Generalised Linear Mixed Models (GLMMs) were used. These are similar to General and Generalised Linear Models, but allow both fixed and random terms to be included. In all mixed models, variance components were estimated using the Restricted Maximum Likelihood (REML) method, and random terms were retained in the model unless the variance component was found to be zero. Where terms correlated (e.g. age and weight), the inclusion of both in the model could lead to spurious measures of significance (Grafen & Hails 2002; Quinn

& Keough 2002). Consequently the term that had a lesser effect was excluded from analysis. In each model, all potential explanatory terms were entered together and then dropped sequentially until only those terms that explained significant variation remained. Repeating the analysis by successive inclusion of significant terms to build a minimal model using the additive method yielded an identical final model in all cases. Each dropped term was then put back into the minimal model to obtain their level of non-significance and to check that significant terms had not been wrongly excluded. All two-way interactions were tested. All statistical tests were two-tailed. Unless otherwise stated, means are quoted ± 1 SE. Where data differed significantly from normality (based on the Anderson-Darling test for normality) data were transformed to attain normality or non-parametric statistics were used.

4.2.5 Competition for food by dominant females with their reproductive competitors.

To investigate competition for food by dominant females with their reproductive competitors, analyses were undertaken to assess the factors that affect how frequently dominant females tried to steal food, how frequently they won competition for food and how aggressive they were during competition for food.

In the first analysis a LMM was used to assess what factors affect how frequently dominant females initiated competition for food. Data were available for the frequency of initiation by dominant females against different categories of individual where they had competed at least once with that category during an observation period. Individuals competed with were categorised into young and old, subordinate males and females. This resulted in a dataset of 402 observation periods on 42 dominant females at 17 different groups. Frequency of initiation was logarithmically transformed and set as the response term in a LMM. The following factors and variables were included as possible explanatory terms: breeding state and average weight of dominant female (g), sex and age category of individual competed with. The average group size and rainfall (factorised as high or low around the mean average rainfall for an observation period) were also included to control for any effect they may have. Repeated measures of group and individual were included in the model as random terms. Residuals from the model were normally distributed.

A GLMM was then used to assess what factors affect the likelihood that dominant females initiating competition for food will be successful. Data were available for the success in competition for food by dominant females with different categories of individual. Individuals competed with were categorised into young and old, subordinate males and females. This resulted in a dataset of 402 observation periods on 42 dominant females at 17 different groups. The number of competitions initiated and won by a dominant female was set as the numerator and the number of competitions initiated by a dominant female was set as the denominator in a binomial GLMM. The factors and random terms were identical to those in the model outlined above.

Finally, a GLMM was used to assess what factors affect how aggressiveness of dominant females during competition for food. Data were available for competition for food events initiated by the dominant female with young and old, subordinate males and females, resulting in a dataset of 1108 competitions for food items. Whether a dominant female contacted (1) or did not contact (0) an individual when initiating competition for food, was set as the binomial response term in a GLMM the binomial denominator was set at 1. The following factors and variables were included as possible explanatory terms: breeding state and weight of dominant female on day (g); sex and age category of individual competed with, and food item size. The group size on the day of interaction, and the total rainfall in the previous three months (mm) were also included to control for any effect they may have. Repeated measures of group, individual and owner were included in the model as random terms.

Experimental Approach in Females

A GLMM was used to assess what factors affect whether the dominant female stole scorpions presented to individuals in their presence or not when she was in different breeding states. However, in order to reduce the number of manipulation experiments undertaken on the meerkat population the experiment outlined in Chapter 3 (3.2.6;

Dominant female) incorporated presentations to individuals intended to answer questions posed in both Chapter 3 and this chapter. In Chapter 3 the consequences of the breeding state of the dominant female for whether she stole a scorpion when pregnant vs when not pregnant from group members was considered. In this chapter, we consider whether dominant females are more likely to steal a scorpion from different categories of contestant (old female, mean age of 823 days; young female, mean age of 454 days; old male, mean age of 643 days), and whether this changes for different categories of contestant when the dominant female is pregnant or not pregnant. Further details of the experiment and analysis may be found in section (3.2.6; *Dominant female*).

4.2.6 Competition for food by dominant males with their reproductive competitors

In the first analysis a LMM was used to assess what factors affect how frequently dominant males initiated competition for food. Data were available for the frequency of initiation by dominant males against different categories of individual where they had competed at least once with that category during an observation period. Individuals competed with were categorised into immigrant and natal, subordinate males and females. This resulted in a dataset of 528 observation periods on 67 dominant male individuals at 24 different groups. Frequency of initiation was logarithmically transformed and set as the response term in a LMM. The following factors and variables were included as possible explanatory terms: average weight of dominant male (g), sex and immigrant status of individual competed with. The average group size and rainfall (factorised as high or low around the mean average rainfall for an observation period) were also included to control for any effect they may have. Repeated measures of group and individual were included in the model as random terms. Residuals from the model were normally distributed.

A GLMM was then used to assess what factors affect the likelihood that dominant males initiating competition for food will be successful. Data were available for the success in competition for food by the dominant male with different categories of individual.

Individuals competed with were categorised into immigrant and natal, subordinate males and females. This resulted in a dataset of 528 observation periods on 67 dominant male individuals at 24 different groups. The number of competitions initiated and won by a dominant male was set as the numerator and the number of competitions initiated by a dominant male was set as the denominator in a binomial GLMM. The factors and random terms were identical to those in the model outlined above.

Finally, a GLMM was used to assess what factors affect the aggressiveness of dominant males during competition for food. Data were available for competition for food events initiated by the dominant male with immigrant and natal, subordinate males and females, resulting in a dataset of 525 competitions for food items. Whether a dominant male contacted (1) or did not contact (0) an individual when initiating competition for food was set as the binomial response term in a GLMM with the binomial denominator set at 1. The following factors and variables were included as possible explanatory terms: weight of dominant male (g); sex and immigrant status of individual competed with, and food item size. The group size on day, and total rainfall in the previous three months were also included to control for any effect they may have. Repeated measures of group, individual and owner were included in the model as random terms.

Experimental Approach in Males

To investigate whether dominant males steal food from their reproductive competitors, analysis of whether dominant males stole scorpions that were presented to individuals in the presence of the dominant male, was undertaken. An adult natal male (>24 months of age), an adult natal female (>24 months of age) and an adult immigrant male (>24 months of age) were presented with a scorpion in the presence of the dominant male. Whether the dominant male successfully stole the scorpion (1) or not (0) from the individual presented with the scorpion was recorded. In total 18 presentations were made in the presence of dominant males at 6 groups, the order of presentations was randomised between groups and scorpion size was standardised (3 grams). A Fishers exact test was used to compare the number of times the dominant male was successful or unsuccessful in stealing the scorpion, when the individual presented with the scorpion was the adult immigrant male or the adult natal male. A Fishers exact test was then used to compare the number of times the dominant male was successful or unsuccessful in stealing the scorpion, when the individual presented with the scorpion was the adult natal male or the adult natal female.

4.2.7 Competition for food by subordinate individuals with their reproductive competitors.

To investigate competition for food by subordinate males and females with their reproductive competitors, analysis of what factors affect how frequently subordinate males and females tried to steal food, how frequently they were successful in competition for food, and how aggressive they were in competition for food they initiated was undertaken. In the first analysis a LMM was used to assess what factors affect how frequently subordinates initiate competition for food. Data were available for the frequency of initiation by subordinate male and female individuals against different categories of individual where they had competed at least once with that category during an observation period. Individuals competed with were categorised by sex as subordinate males or females. This resulted in a dataset of 747 observation periods on 649 subordinate individuals at 17 different groups. Frequency of initiation was logarithmically transformed and set as the response term in a LMM. The following factors and variables were included as possible explanatory terms: sex and average weight of subordinate (g), and sex of individual competed with. The average group size, and rainfall (factorised as high or low around the mean average rainfall during an observation period) were also included to control for any effect they may have. Repeated measures of group and individual were included in the model as random terms. Residuals from the model were normally distributed.

A GLMM was then used to assess what factors affect the likelihood that subordinate males and female initiating competition for food will be successful. Data were available for the success in competition for food by subordinate males and females with different categories of individual. Individuals competed with were categorised by sex as subordinate males or females. This resulted in a dataset of 747 observation periods on 649 subordinate individuals at 17 different groups. The number of competitions initiated and won by a subordinate individual was set as the numerator and the number of competitions initiated by a subordinate individual was set as the denominator in a binomial GLMM. The factors and random terms were identical to those in the model outlined above.

Finally, a GLMM was used to assess what factors affect the aggressiveness subordinate individuals during competition for food. Data were available for competition for food events initiated by subordinate individuals with subordinate males and females, resulting in a dataset of 1341 competitions for food items. Whether a subordinate individual contacted (1) or did not contact (0) an individual when initiating competition for food was set as the binomial response term in a GLMM with the binomial denominator set at 1. The following factors and variables were included as possible explanatory terms: weight (g) and sex of individual; sex of individual competed with, and food item size. The group size on day, and total rainfall in the previous three months (mm) were also included to control for any effect they may have. Repeated measures of group, individual and owner were included in the model as random terms.

Experimental Approach in Subordinates

To investigate whether subordinate males and females steal food from their future reproductive competitors. I tested whether subordinate males or females stole scorpions presented to individuals in the presence of the subordinate males or females. Where litters of two male and two female adult individuals occurred in their natal group, a scorpion was presented separately to a male littermate and a female littermate in the presence of their female and then their male littermate, resulting in a dataset of 24 presentations at 6 groups. Whether the littermate male was successful in stealing the scorpion (1) or not (0) from the littermate presented with the scorpion was recorded, A Fishers exact test was used to compare the number of times the subordinate male was successful or unsuccessful in stealing the scorpion, when the individual presented with the scorpion was the same or opposite sexed littermate. A Fishers exact test was also used to compare the number of times the subordinate female was successful or unsuccessful in stealing the scorpion, when the individual presented with the scorpion was the same or opposite sexed littermate.

4.3 RESULTS

4.3.1 Competition for food by dominant females with their reproductive competitors

Dominant females did not initiate competition for food more frequently with females than males (controlling for the significant positive effect of breeding state, rainfall, age of individual competed with and the significant negative effect of group size LMM: $\chi^2 = 1.37$, $P = 0.242$; Table 4.1). However, dominant females were significantly more likely to be successful in competition for food with females than males (GLMM: $\chi^2 = 27.53$, $P = <0.001$; Table 4.2; Fig. 4.1.a), after controlling for the significant positive effect of breeding state and negative effect of dominant female weight. Furthermore, the dominant female was more likely to be successful in competition for food with females when pregnant, whilst there was no similar increase in the likelihood that they would steal a scorpion from males (GLMM interaction: $\chi^2 = 6.87$, $P = 0.032$; Table 4.2; Fig. 4.1.b). Experimental presentations of scorpions to individuals in the presence of the dominant female show that dominant females are more likely to steal a scorpion from old females than young females or males, and more likely to steal a scorpion from young females than males (GLMM: $\chi^2 = 9.14$, $P = 0.010$; Chapter 3; Table 3.5; Fig. 4.2) once the significant positive effects of breeding state and scorpion size have been accounted for. An interaction between category of individual competed with and breeding state may have been expected if the increase in success by the dominant female when pregnant was larger against females than males. However, no significant interaction was found, which may be a result of a comparatively small sample size. When the dominant female was pregnant compared with when not pregnant, the increase in the number of scorpions stolen from old and young females was larger than the increase in the number stolen from old males (Fig. 4.3).

Dominant females initiated contact aggression in competition for food with females more frequently than when they were competing with males (GLMM: $\chi^2 = 4.36$, $P = 0.037$; Table 4.3; Fig. 4.4.a), after controlling for the significant negative effect of group size. In addition they were more likely to initiate contact aggression in competition for food with old females than young females but were less likely to do so against old males than young males (GLMM interaction: $\chi^2 = 5.60$, $P = 0.018$; Table 4.3; Fig. 4.4b).

Table 4.1. LMM (with an identity link function) of the terms affecting how frequently dominant females initiate competition for food

Full model		**F statistic (χ^2)**	**d.f**	***P***
Group size		67.36	1	<0.001
Age of competitor		59.58	1	<0.001
Breeding state (lactating, pregnant, non breeding)		23.61	2	<0.001
Rainfall (high, low)		19.78	1	<0.001
Weight (g)		1.98	1	0.159
Sex of competitor		1.37	1	0.242
Minimal model		**Effect**	**S.E.**	
Constant		-3.81	0.06	
Group size		-0.03	0.003	
Age of competitor	Young	0.00	0.05	
	Old	0.35	0.06	
Breeding state	Lactating	0.00	0.06	
	Pregnant	-0.11	0.06	
	Non breeding	-0.21	0.06	
Rainfall	High	0.00	0.06	
	Low	0.16	0.05	

Group (component±SE=0.01±0.01), and initiator (0.02±0.01) were included as random terms in the model.

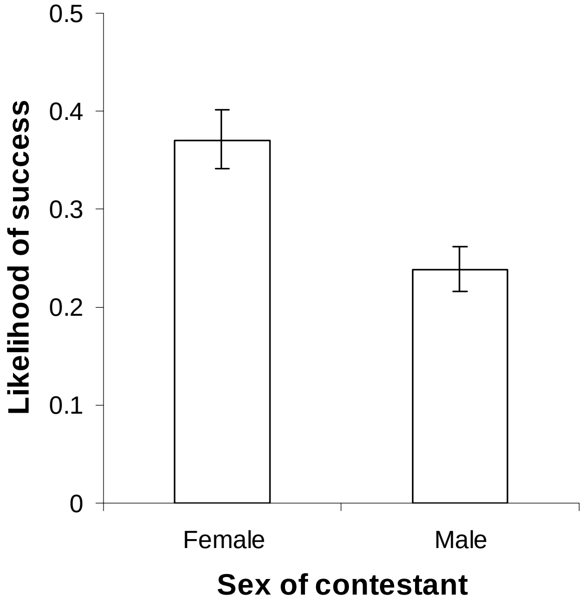
Table 4.2. GLMM (with a binomial distribution and a logit link function) of the terms affecting how successful dominant females are in competition for food

Full model		**Wald statistic (χ^{2})**	**d.f**	***P***
Sex of competitor		27.53	1	<0.001
Breeding state (lactating, pregnant, non breeding)		17.12	2	<0.001
Weight (g)		8.04	1	0.005
Breeding state * sex of competitor		6.87	2	0.032
Age of competitor		1.78	1	0.138
Rainfall (high, low)		1.30	1	0.255
Group size		0.95	1	0.329
Minimal model		**Effect**	**S.E.**	
Constant		-0.12	0.19	
Sex of competitor	Female	0.00	0.13	
	Male	-0.62	0.13	
Breeding state	Lactating	0.00	0.16	
	Pregnant	-0.35	0.15	
	Non breeding	-0.88	0.16	
Weight		0.003	0.001	
Breeding state * sex of competitor		See Fig. 4.1.b		

Group (component±SE=0.03±0.08), and initiator (0.08±0.09) were included as random terms in the model.

Figure 4.1. The affect of (a) the sex of the individual and (b) breeding state when competing with males or females on how frequently the dominant female is successful in competition for food. All graphs show predicted means and standard errors from a GLMM controlling for the effects of significant terms and random terms listed in Table 4.2.

(a)



(b)

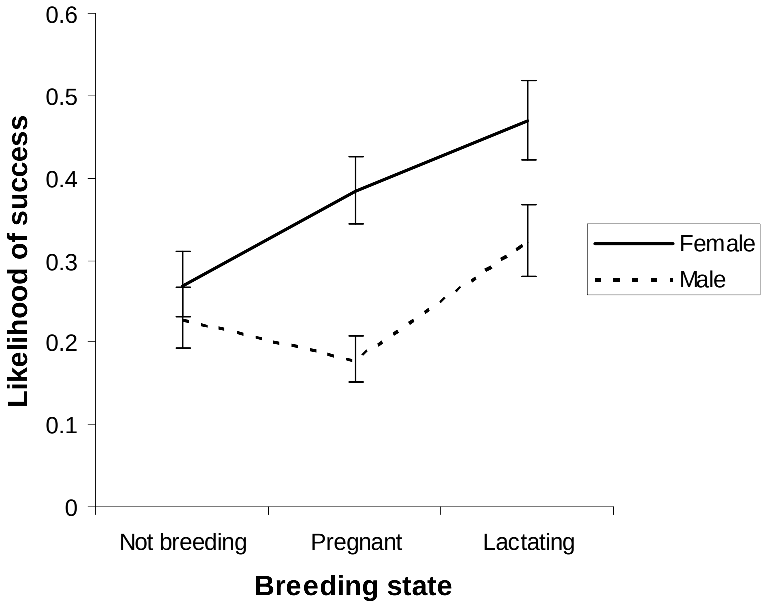


Figure 4.2. The affect of the category of individual presented with a scorpion, on the likelihood that the dominant female stole a scorpion. All graphs show predicted means and standard errors from a GLMM controlling for the effects of significant terms and random terms listed in Chapter 3; Table 3.5.

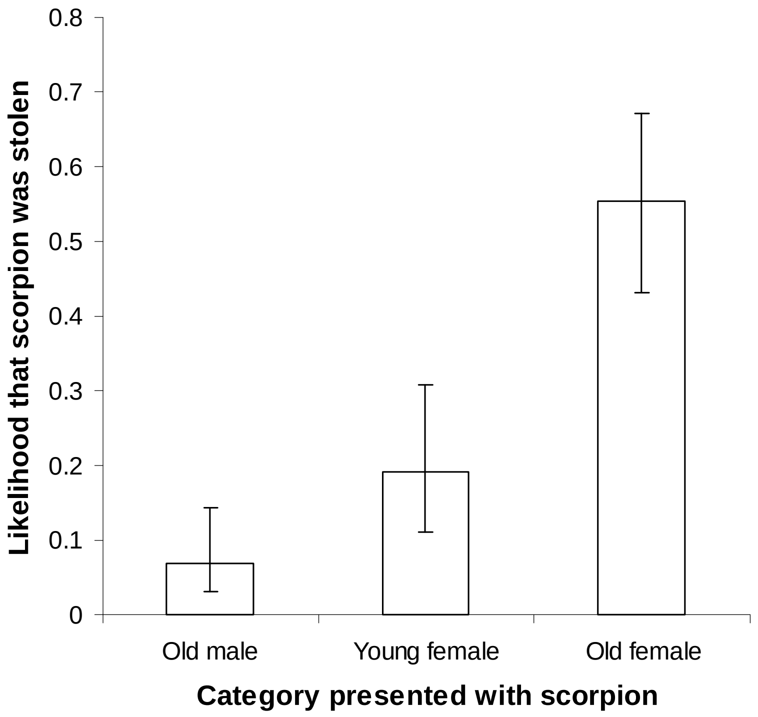


Figure 4.3. Shows the number of scorpions stolen by the dominant female when not pregnant and pregnant, from different categories of individuals divided by the number of scorpions presented to that category.

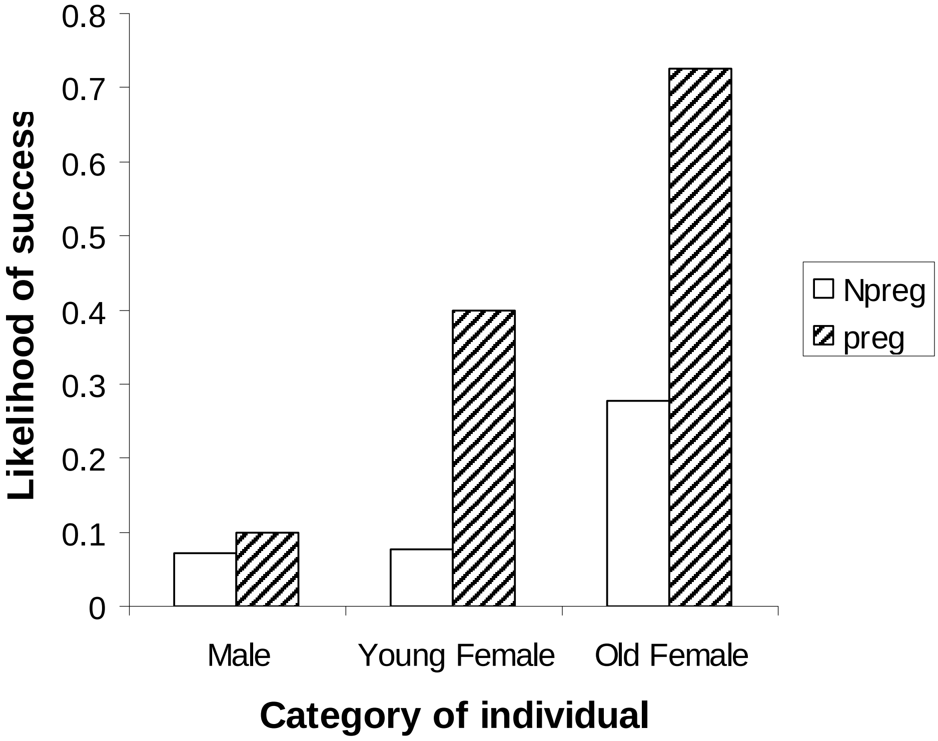


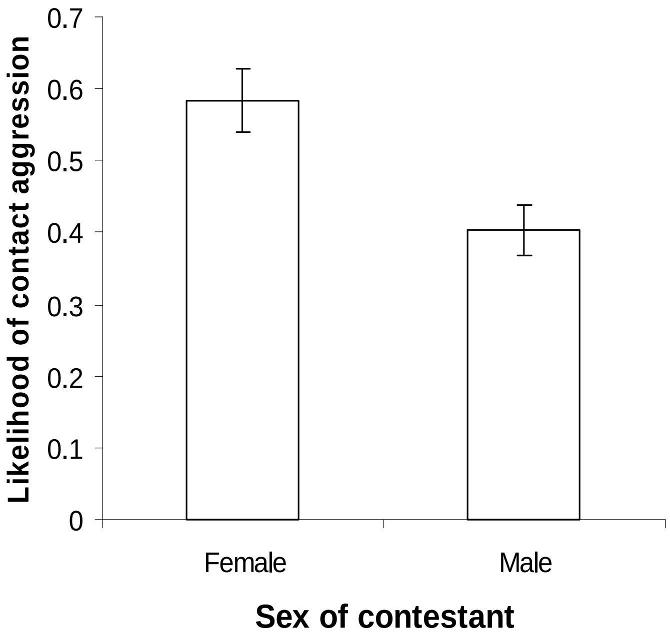
Table 4.3. GLMM (with a binomial distribution and a logit link function) of the terms affecting how aggressive dominant females are in competition for food

Full model		**Wald statistic (χ^2)**	**d.f**	***P***
Group size		6.33	1	0.012
Sex of competitor * age of competitor		5.60	1	0.018
Sex of competitor		4.36	1	0.037
Breeding state (lactating, pregnant, non breeding)		2.91	2	0.234
Weight (g)		1.07	1	0.301
Age of competitor		0.17	1	0.680
Rainfall (high, low)		0.01	1	0.921
Minimal model		**Effect**	**S.E.**	
Constant		-0.05	0.10	
Group size		0.024	0.01	
Sex of competitor * age of competitor		See Fig. 4.4.b		
Sex of competitor	Female	0.00	0.18	
	Male	-0.20	0.15	

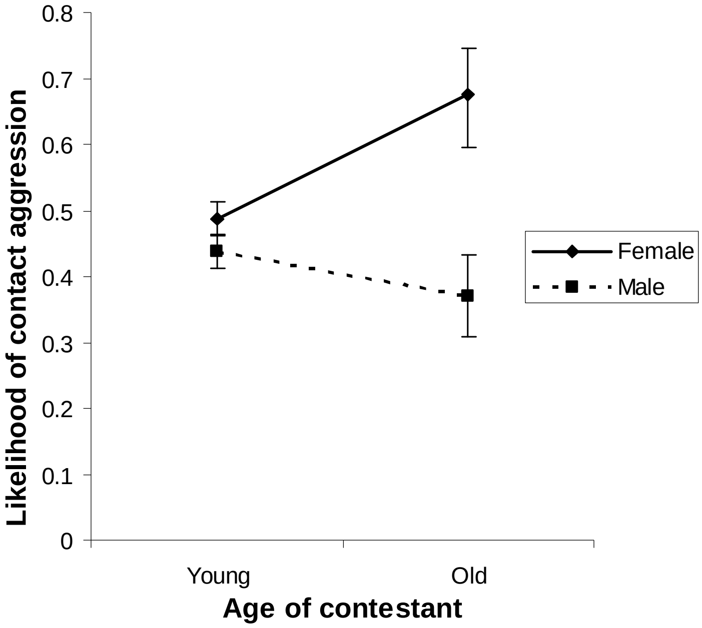
Owner (0.27±0.11) was included as a random term in the model.

Figure 4.4. The affect of (a) the sex of the individual and (b) the age of competitor when competing with males or females, on how frequently the dominant female initiates contact aggression in competition for food. All graphs show predicted means and standard errors from a GLMM controlling for the effects of significant terms and random terms listed in Table 4.3.

(a)



(b)



4.3.2 Competition for food by dominant males with their reproductive competitors

Dominant males initiated competition for food more frequently with immigrant individuals than with natal individuals (LMM: χ^2_1 = 52.87, *P* = <0.001; Table 4.4) accounting for the significant negative effect of group size. However, they were not more likely to initiate competition with males than females (LMM: χ^2_1 = 0.02, *P* = 0.901; Table 4.4), or with immigrant males than natal males (LMM interaction: χ^2_1 = 0.0, *P* = 0.997; Table 4.4). Dominant males were also more likely to be successful in competition for food with immigrant individuals than natal individuals (GLMM: χ^2_1 = 3.86, *P* = 0.049; Table 4.5), but were not more likely to be successful in competition for food with males than females (GLMM: χ^2_1 = 0.30, *P* = 0.583; Table 4.5), or with immigrant males than natal males (GLMM interaction: χ^2_1 = 1.23, *P* = 0.268; Table 4.5). There was no evidence to suggest that dominant males initiated contact aggression in competition for food with males more frequently than with females, or with immigrant males than natal males (GLMM interaction: χ^2_1 = 1.72 *P* = 1.90; Table 4.6), after controlling for the negative effect of dominant male weight (GLMM: χ^2_1 = 0.24, *P* = <0.623; Table 4.6). The dominant male was not significantly more likely to steal a scorpion from immigrant males than natal males (Fishers exact test *P* = 0.5) or from natal males than from natal females (Fishers exact test: *P* = 0.842).

Table 4.4. LMM (with an identity link function) of the terms affecting how frequently dominant males initiate competition for food

Full model		**F statistic (χ^2)**	**d.f**	***P***
Immigrant status of competitor (natal, immigrant)		52.87	1	<0.001
Group size		7.08	1	0.008
Rainfall (high, low)		2.67	1	0.102
Weight (g)		1.07	1	0.301
Sex of competitor		0.02	1	0.901
Sex of competitor * immigrant status of competitor		0.00	1	0.997
Minimal model		**Effect**	**S.E.**	
Constant		-3.80	0.06	
Immigrant status of competitor	Immigrant	0.00	0.07	
	Natal	-0.45	0.05	
Group size		-0.01	0.004	

Group (component±SE=-0.0004±0.01), and initiator (0.05±0.02) were included as random terms in the model.

Table 4.5. GLMM (with a binomial distribution and a logit link function) of the terms affecting how frequently dominant males are successful in competition for food

Full model		**Wald statistic (χ^2)**	**d.f**	***P***
Immigrant status of competitor (natal, immigrant)		3.86	1	0.049
Sex of competitor * immigrant status of competitor		1.23	1	0.268
Weight (g)		0.50	1	0.478
Sex of competitor		0.30	1	0.583
Rainfall (high, low)		0.04	1	0.850
Group size		0.01	1	0.926
Minimal model		**Effect**	**S.E.**	
Constant		-0.86	0.20	
Immigrant status of competitor	Immigrant	0.00	0.20	
	Natal	-0.46	0.16	

Group (component±SE=0.05±0.09), was included as a random term in the model.

Table 4.6. GLMM (with a binomial distribution and a logit link function) of the terms affecting how aggressive dominant males are in competition for food

Full model	**Wald statistic (χ^2)**	**d.f**	***P***
Weight (g)	12.43	1	<0.001
Food item size (hole, small, large)	3.92	2	0.141
Group size	2.09	1	0.149
Sex of competitor * immigrant status of competitor	1.72	1	0.190
Immigrant status of competitor (natal, immigrant)	1.21	1	0.272
Rainfall (high, low)	0.45	1	0.502
Sex of competitor	0.24	1	0.623
Minimal model	**Effect**	**S.E.**	
Constant	-0.27	0.12	
Weight	-0.006	0.002	

Group (component±SE=0.003±0.07), and owner (0.34±0.21) were included as random terms in the model.

4.3.3 *Competition for food by subordinate males and females with their reproductive competitors*

Subordinate females initiated competition for food more frequently than subordinate males (LMM: $\chi^2_1 = 4.11$, $P = 0.043$; Table 4.7) controlling for the significant negative effect of group size, which may be due to higher costs of reproduction in females than males. Interestingly, subordinate males and females initiated competition for food more frequently with opposite-sex subordinate group members than with their same-sex group members (LMM interaction: $\chi^2 = 22.51$, $P = <0.001$; Table 4.7; Fig. 4.5). There was no significant difference between males and females in the likelihood that they would be successful in competition for food (GLMM: $\chi^2 = 0.02$, $P = 0.894$; Table 4.8) controlling for the significant negative effect of weight, nor was there any evidence that subordinate individuals were more likely to be successful in competition for food with either same or opposite sex group members (GLMM interaction: $\chi^2 = 0.17$, $P = 0.684$; Table 4.8). There was no significant difference in the likelihood that males or females initiate contact aggression in competition for food (GLMM: $\chi^2_1 = 0.88$, $P = 0.348$; Table 4.9) after controlling for the significant negative effect of group size. Furthermore there was no evidence that subordinate males or females were more likely to initiate contact aggression in competition for food with same or opposite sex individuals (GLMM interaction: $\chi^2_1 = 0.43$, $P = 0.510$; Table 4.9).

In 24 experimental presentations of scorpions to subordinate males and females in the presence of opposite and same sexed littermates, no scorpions were successfully stolen from the individual presented with the scorpion. Therefore, neither subordinate males, nor subordinate females were more likely to steal a scorpion from the same or opposite sexed littermates (Fishers exact test: Males with litter mates $P = 0.5$; Females with litter mates $P = 0.5$).

Table 4.7. LMM (with an identity link function) of the terms affecting how frequently subordinate individuals initiate competition for food

Full model		**Wald statistic ($\chi^{2)}$**	**d.f**	***P***
Group size		237.31	1	<0.001
Sex * Sex of competitor		22.51	1	<0.001
Rainfall (high, low)		4.14	1	0.042
Sex		4.11	1	0.043
Weight (g)		0.93	1	0.334
Sex of competitor		0.69	1	0.408
Minimal model		**Effect**	**S.E.**	
Constant		-4.55	0.04	
Group size		-0.03	0.002	
Sex * Sex of competitor		See Fig. 4.5		
Rainfall	High	0	0.03	
	Low	0.05	0.03	
Sex	Female	0	0.03	
	Male	0.07	0.03	

Group (component±SE=0.007±0.004), and initiator (0.01±0.005) were included as random terms in the model.

Figure 4.5. The affect of the sex of the individual when competing with male or female individuals, on how frequently subordinates initiate competition for food. All graphs show predicted means and standard errors from a GLMM controlling for the effects of significant terms and random terms listed in Table 4.7.

Table 4.8. GLMM (with a binomial distribution and a logit link function) of the terms affecting how frequently subordinate individuals are successful in competition for food

Full model	**Wald statistic (χ^2)**	**d.f**	***P***
Weight (g)	6.38	1	0.012
Sex of competitor	3.59	1	0.058
Sex * sex of competitor	0.17	1	0.684
Rainfall (high, low)	0.09	1	0.768
Sex	0.02	1	0.894
Group size	0.01	1	0.919
Minimal model	**Effect**	**S.E.**	
Constant	-2.57	0.15	
Weight	0.003	0.001	

Group (component±SE=0.10±0.12), and initiator (1.76±0.31) were included as random terms in the model.

Table 4.9. GLMM (with a binomial distribution and a logit link function) of the terms affecting how aggressive subordinate individuals are in competition for food

Full model	**Wald statistic (χ^2)**	**d.f**	***P***
Group size	18.46	1	<0.001
Food size	4.98	2	0.083
Sex	0.88	1	0.348
Sex * sex of competitor	0.43	1	0.510
Sex of competitor	0.24	1	0.625
Weight (g)	0.06	1	0.808
Rainfall (high, low)	0.00	1	0.987
Minimal model	**Effect**	**S.E.**	
Constant	-0.63	0.08	
Group size	0.04	0.009	

Group (component±SE=0.03±0.04), initiator (0.17±0.10) and owner (0.09±0.09) were included as random terms in the model.

4.4 DISCUSSION

The success of dominant females in competition for food reflects patterns of reproductive conflict. Dominant females were more likely to be successful in competition for food with other females, and success increased when the dominant female was pregnant, whilst there was no change in their success against males. It is unlikely that increased success against females when pregnant is a consequence of the nutritional demands of pregnancy as they would be expected to be more successful in competition for food with all group members, and not just females. Experimental presentations of food items to individuals in the presence of the dominant female also showed that dominant females were more likely to steal scorpions from females than males and old females than young females. Dominant females reproductively suppress subordinate females, showing higher levels of aggression towards them than to males, particularly towards the eldest females in the group (Kutsukake & Clutton-Brock 2006; Young *et al* 2006). Aggression intensifies when dominant females are pregnant ultimately leading to the eviction of females starting with the eldest (Clutton-Brock *et al* 2001b; Kutsukake & Clutton-Brock

2006; Young *et al* 2006). Therefore the success of the dominant female in competition for food with their reproductive competitors, especially during periods when reproductive conflict is most intense, reflects patterns of reproductive suppression.

Reproductive conflict may affect competition for food in two ways; firstly, dominant females may be more aggressive in competition for food with their reproductive competitors. Secondly, the reproductive competitors of the dominant female may avoid conflict with her. Either of these could contribute to reproductive suppression. Dominant females were more aggressive in competition for food with females than males, and were more aggressive in competition for food with old females than other group members. Consequently, increased aggression by the dominant female partially explains why they are more successful in competition for food with their reproductive competitors, particularly old females. However, there was no overall increase in aggression by dominant females when they were pregnant. Therefore, dominant females may be more successful in competition for food when pregnant than when not pregnant because subordinate females reduce the defence of food items. Previous studies of patterns of grooming (Kutsukake & Clutton-Brock 2006a) and submission (Kutsukake & Clutton-Brock 2006b) suggest that subordinate females, especially old females, may try to placate the dominant female when she is pregnant. This is because conflict between subordinate and dominant females during pregnancy could result in a subordinate female being evicted from the group (Young *et al* 2006). Subordinate females are likely to incur high costs from eviction as a result of weight loss, abortion (Young *et al* 2006), and possibly increased threat of predation (Clutton-Brock *et al* 1999a). Dominant females may be more successful in competition for food with their reproductive competitors, partially as a consequence of subordinate females relinquishing their food to avoid conflict. However, the dominant female was more aggressive in competition for food with her reproductive competitors, particularly old subordinate females, with whom they are in greatest reproductive conflict. Therefore, competition for food could be a cause of reproductive suppression.

I initially suggested that competition for food could function as a mechanism of reproductive suppression, by contributing to aggression directed towards reproductive competitors or by depriving them of nutritional resources. It is unlikely that competition for food deprives reproductive competitors of significant nutritional resources as the frequency of competition for food was very low (Chapter 2). Furthermore, dominant females did not compete for food more frequently with their reproductive competitors, possibly due to restrictions on the opportunity to compete for food, particularly with specific group members. Individuals infrequently locate large, contestable food items and may not be close to their reproductive competitors when they find them as a result of group dispersion (Doolan & Macdonald 1996a). However, competition for food could function as an additional means of dominance assertion by dominant females over their reproductive competitors. It has been shown that aggression in competition for food by the dominant female with their reproductive competitors accurately reflects patterns of dominance assertion and eviction which are behavioural tactics employed by the dominant female in reproductive suppression (Kutsukake & Clutton-Brock 2006b; Young *et al* 2006). Furthermore absolute frequency of dominance assertions by dominant females against subordinate females (0.08 assertions per hour, Kutsukake & Clutton-Brock 2006) is similar to the frequency of competition for food by dominant females with subordinate females (0.05 ±0.04 competitions for food per hour; mean, S.D.). It is therefore possible that competition for food may contribute to the suppression of reproductive competitors by dominant individuals in species with high reproductive conflict. This is the first study showing that competition for food may play a role in reproductive suppression.

There was no indication that reproductive conflict has any consequences for patterns of competition for food by dominant males, subordinate males, or subordinate females. The primary reproductive competitors of the dominant male in the group are subordinate immigrant males who may breed with the dominant female (Griffin *et al* 2003) and are the principle recipients of aggression from by the dominant male (Kutsukake & Clutton-Brock I*n press*). However, there was no evidence that dominant males initiated more competition for food, were more successful in competition for food or were more aggressive in competition for food with subordinate immigrant males than with other group members. Reproductive conflict is therefore unlikely to have any significant consequences for competition for food by the dominant male in meerkat groups. Subordinate males and females typically compete aggressively for the dominance position with same sex subordinate group members when a position becomes available (Sharpe 2005; Clutton-Brock *et al* 2006). Subordinate males and females were not more successful or more aggressive in competition for food with same sex subordinate group members. However, both subordinate males and females were less likely to initiate competition for food with their same sex litter mate, contrary to the expectation that they would compete for food more frequently with their likely future reproductive competitors. Same sex subordinate individuals occasionally initiate low aggression stereotyped competitive behaviour typified by pushing their bodies against each other or rubbing muzzles (Clutton-Brock *unpublished data*) where neither individual submits. They may therefore avoid initiating competition for food with their future reproductive competitors as the cost of competition could be higher where the contestant is less likely to back down (Maan *et al* 2001). Reproductive conflict is therefore unlikely to increase the extent of competition for food by dominant males and subordinates with their reproductive competitors, in contrast to large effects of reproductive conflict on competition for food by dominant females with their reproductive competitors.

The effect of reproductive conflict on patterns of competition for food by dominant females, dominant males and subordinates is likely to reflect variation in the intensity of reproductive conflict. In meerkats, reproductive skew is greatest amongst females (Clutton-Brock *et al* 2006), as a result of the long dominance tenure of dominant females and because subordinate females are restricted to breeding within their group (Griffin *et al* 2003; Clutton-Brock *et al* 2006). Competition for the opportunity to breed between females results in sexual selection for traits which increase female competitive ability, that are absent in males (Clutton-Brock *et al* 2006). In particular, when subordinate females are pregnant they may kill the dominant females offspring (Young & Clutton-Brock 2006), and so the dominant female exhibits behaviours that reproductively suppress subordinate female breeding (Clutton-Brock *et al* 2001b; Young *et al* 2006).

Therefore, reproductive conflict in meerkats is greatest between dominant and subordinate females which may explain patterns of competition for food by dominant females and their competitors that are absent between other group members. Dominant female meerkats may use aggression in competition for food to reinforce their dominance. This may be a result of sexual selection for traits that increase competitive ability (Clutton-Brock *et al* 2006) and contribute to reproductive suppression (Faulkes & Abbott 1997; Williams 2004; Kutsukake & Clutton-Brock 2006; Young 2006). Competition for food could therefore have been overlooked as a potential means by which dominant individuals in cooperatively breeding species could assert their dominance as a means of reproductive suppression.

CHAPTER 5 - *General Discussion*

This study provides insight into what determines whether group members win competition for food, and why they initiate competition for food. Furthermore, this was the first study of competition for food in a cooperatively breeding species with a despotic dominance system. This revealed the important consequences of reproductive conflict and reproductive skew for competition for food in group living species.

5.1 What decides the outcome of competition for food

In meerkats, competition for food resources between group members is decided by asymmetries between contestants. In particular, asymmetries in ownership of a resource typically decided the outcome of competition for food between group members. It is likely that this is a consequence of the comparatively low benefits of competition since food distribution does not favour monopolization and group members competed infrequently (Doolan & Macdonald 1996a). Maynard-Smith (1982) predicted that group members may show respect for ownership in competition for resources avoiding frequent and costly conflict between group members. These results therefore provide empirical support for theoretical models of the factors that decide the outcome of contests over resources in group living species. However, large asymmetries between group members in dominance status (Resource Holding Potential, RHP) or the value of a resource (Resource Value, RV) also contributed to the outcome of competition. Dominant individuals were more successful in competition for food than subordinates. This is likely to be a consequence of asymmetries in their fighting ability or RHP, which is commonly denoted by dominance status (Parker 1974a; Maynard-Smith & Parker 1976; Hammerstein 1981). Females were more successful in competition for food when breeding (Fig. 3.3.b), particularly the dominant female, who has the highest costs of reproduction in the group in cooperatively breeding species (Creel & Creel 1991; Clutton-Brock 2001b). This indicates that asymmetries in RV to group members resulting from the costs of reproduction to females were also important in deciding the outcome of competition for food (Parker 1974a; Maynard-Smith & Parker 1976; Ewald & Rohwer 1980). These results support theoretical predictions that large asymmetries may decide the outcome of competition irrespective of other asymmetries between contestants (Grafen 1987). Furthermore, conflict between specific individuals is determined by asymmetries in ownership of a resource, RHP and RV, that all contribute to determine the outcome of the contest (Maynard-Smith 1976).

5.2 Why do individuals compete for food

Meerkats competed infrequently for food, but they did vary how frequently they tried to steal food in response to variation in the costs of competition and their own nutritional demands. Infrequent stealing is likely to be a result of there being few opportunities for competition where food is widely distributed and typically of low value (Doolan & Macdonald 1996a). Consequently no group members operated a ‘scrounger’ foraging strategy foregoing self foraging (Barnard & Sibly 1981; Coolen 2002). However, there was variation in the frequency with which group members initiated competition for food. This provides an insight into the factors that affect the costs and benefits of competition.

Meerkats initiated competition for food more frequently when the costs of conflict were low or the value of a resource to them was high. Dominant meerkats are more likely to be successful and may suffer lower costs of conflict with subordinates, and consequently they stole food more frequently. Group members also tried to steal more food where it was more valuable to them. Trivers (1972) predicted that competition for food would be more intense amongst females than males as a result of asymmetries in the costs of reproduction (Williams 1966; Creel & Creel 1991). Results supported this prediction as females competed for food more frequently than males and more frequently when breeding.

Group members that may have been less able to find food (Clutton-Brock *et al* 2001a) or closer to starvation (Neuhaus 2000) tried to steal more food. In addition, all group members tried to steal more food when rainfall was low, and in the Kalahari low rainfall is associated with a reduction in food availability (Seely & Louw 1980; Pianka 1986; Doolan and Macdonald 1996a; Turbe 2006). Furthermore, meerkats in small groups competed more frequently than individuals in large groups, even when rainfall was high. This result runs contrary to predictions about competition for food in group living species which suggest that competition will be more intense in larger groups where food resources are more depleted (Sirot 2000; Saj & Sicotte 2007). However, meerkats are cooperative breeders and consequently individuals in small groups may undertake more costly helping behaviour per individual than individuals in large groups (Clutton-Brock *et al* 1998a, Clutton-Brock *et al* 2001a). This may be particularly acute during the rainy season when meerkats typically breed (Doolan & Macdonald 1997b; Clutton-Brock *et al* 1999b). Therefore, in cooperatively breeding species, individuals in small groups compete for food more frequently than individuals in large groups.

Consequently, group members tried to steal more food when it was likely to be more beneficial to them, which indicated that they may alter their behavioural strategies in response to variation in their immediate nutritional demands. Further research should investigate the mechanisms that enable individuals to monitor their energetic state and consequently respond with adaptive behaviours such as increased competition for food where it is more valuable. This study also indicates what factors are likely to affect the benefit of resources to individual group members and group members as a whole. This may have important consequences for the foraging strategies of different group members in species where the opportunity to compete for food is common. Finally, where all group members have increased nutritional demands, frequent and costly conflict for food between group members could impose high costs on group members, reducing group cohesion. This could contribute to dispersal decisions in species where conflict is intense and food may be monopolized.

5.3 Reproductive skew, reproductive conflict and competition for food

Reproductive conflict and reproductive skew have important consequences for patterns of competition for food in the cooperatively breeding meerkat. Competition for the opportunity to breed has resulted in intense reproductive conflict and high reproductive skew between group members (Clutton-Brock 1998; Clutton-Brock *et al* 2006). The dominant male and female monopolize reproduction and prevent subordinate individuals from breeding (Creel *et al* 1992; Keller & Reeve 1994; Creel & Macdonald 1995; Clutton-Brock *et al* 2001b). In particular, dominant females employ a range of behavioural tactics to suppress the breeding of their reproductive competitors (Clutton-Brock *et al* 2006; Young *et al* 2006). Consequently, asymmetries exist between group members in dominance status which are likely to explain why the dominant male and female steal more food than subordinate group members. Furthermore, the dominant breeding female may have higher energetic costs of reproduction than subordinate females as a result of their high reproductive rates and the costs of reproduction in cooperatively breeding species (Creel & Creel 1991; Clutton-Brock *et al* 2001b). This may explain why the dominant female stole more food than any other group members, particularly when they were lactating. Future studies should consider the importance of competition for food to different female group members in species with high reproductive skew.

In meerkats, reproductive conflict is particularly intense amongst females as they have greater reproductive skew than males (Clutton-Brock *et al* 2006). The dominant female employs a range of aggressive behavioural tactics to suppress the breeding of their reproductive competitors (Clutton-Brock *et al* 2006; Young *et al* 2006). As a result the likelihood that the dominant female will be successful in competition for food with different group members accurately reflects the extent to which they are reproductively suppressed. This is likely to be a consequence of the dominant female being more aggressive when competing for food with their reproductive competitors, and the competitors of the dominant female relinquishing food items to avoid costly conflict (Kutsukake & Clutton-Brock 2006a, b). Competition for food could therefore function as a mechanism of dominance assertion over subordinate females, contributing to their reproductive suppression (Creel *et al* 1992; Moss *et al* 2001; Kutsukake & Clutton-Brock 2006b; Young *et al* 2006).

This study therefore provides evidence that competition for the opportunity to breed between group members may have important consequences for the costs and benefits of competition for food. It is possible that competition for food is a behavioural trait under multiple selective pressures in meerkats. Dominant females steal more food when breeding and steal more food from their reproductive competitors; competition for food could therefore contribute to both reproductive success and competitive ability. Future studies should investigate competition for food resources in a cooperatively breeding species with a despotic dominance hierarchy, where the distribution of food favours its monopolisation by group members. Under these circumstances, dominant individuals may use competition for food as a behavioural tactic that both increases their own breeding success and reproductively suppresses their competitors by depriving them of resources.

5.4 General Conclusions

In this study, long term behavioural observations and controlled experiments enabled the detailed investigation of competition for food in a group living species. Results confirmed theoretical predictions that asymmetries between group members decide the outcome of competition for food (Maynard-Smith & Parker 1976; Maynard-Smith 1982). In meerkats, competition for food is unlikely to be a behavioural tactic with large energetic benefits (Barnard & Sibly 1981) since there are infrequent opportunities to compete for food. However, group members did compete for food more frequently where the costs of competition were low or the benefits were high. This provided insight into the factors that may affect whether group members try to steal food. In particular competition for food may be important for female reproduction as a consequence of asymmetries in the benefits of food to female and male reproductive success (Trivers 1972).

This study was the first to investigate competition for food in a cooperatively breeding species with a despotic dominance hierarchy (Clutton-Brock 1998). It was shown that where reproductive skew and reproductive conflict are high, these may have important consequences for competition for food. Competition for food may therefore be a behavioural trait under multiple selective pressures in species with high reproductive skew and intense reproductive conflict.

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