CHAPTER SIX

# Demography and Social Evolution of Banded Mongooses

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# 1. INTRODUCTION

## 1.1. Cooperative Breeders and the Study of Social Evolution

Long-term studies of cooperatively breeding birds and mammals have been enormously valuable in the search for the general principles about how social behavior and animal societies evolve. These systems have an enduring appeal for researchers for several reasons. First, they provide clear-cut examples of helping (i.e. behavior that boosts the fecundity of other breeders) together with the opportunity to measure the lifetime consequences of variation in helping effort, and hence an opportunity to test theories about how cooperation and altruism can evolve and persist in the face of selection for self-interest. Second, within groups some individuals obtain a disproportionate share of the benefits of teamwork, leading to inherent genetic conflicts of interest, which represent a barrier to stable and peaceful cooperation. Studies of wild cooperative breeders have helped to reveal the ecological and genetic factors that can inhibit or eliminate selection for costly selfish acts in cooperative groups, with broad relevance for the evolution of cooperation. Third, research on these species has helped to understand the evolution of the unusual human life history, many features of which (e.g. short interbirth interval, long period of offspring dependency, decoupled rates of reproductive and somatic senescence) appear to reflect an evolutionary history of cooperative breeding (Cant & Johnstone, 2008; Hawkes, O'Connell, Blurton-Jones, Alvarez, & Charnov, 1998; Kaplan, Hooper, & Gurven, 2010; Mace & Sear, 2005). Finally, cooperative breeding systems continue to intrigue because even basic questions about the social behavior and social structure of cooperative breeders remain poorly understood. Why do some helpers work much harder than others? Why do dominant individuals monopolize reproduction in some species but not in others? What determines individual patterns of dispersal and mating, and what are the consequences of this variation in demography for social evolution and behavior?

Progress on understanding the evolution of helping and conflict resolution has not been hampered by a lack of theoretical models of social evolution. Hamilton's (1964) inclusive fitness theory in particular provides a very broad conceptual framework to understand the genetic and social conditions that promote the helping behavior; while ecological constraints models have proved successful in explaining why an offspring can gain from a delayed dispersal (Dickinson & Hatchwell, 2004; Emlen, 1982, 1995; Hamilton, 1964; Koenig, Pitelka, Carmen, Mumme, & Stanback, 1992). However, broad-brush models of inclusive fitness and ecological constraints have proved less useful at explaining detailed patterns of social behavior within groups, or the evolutionary causes of variation in social structure across species. For example, kin selection on its own has trouble explaining large differences in helping the effort among individuals of the same age, sex, condition, and genetic relatedness (Field & Cant, 2009; Griffin & West, 2003), and the presence of unrelated, hardworking helpers in some insect and vertebrate societies (Leadbeater, Carruthers, Green, van Heusden, & Field, 2010; Queller et al., 2000) suggests that individual variation in helping may be driven by coercion or delayed fitness benefits. In the study of reproductive skew, early hopes that "transactional" models might provide a universal explanation for variation in skew within and between species have faded due to a lack of empirical support, particularly in the case of skew among female vertebrates (Cant, Hodge, Gilchrist, Bell, & Nichols, 2010; Clutton-Brock et al., 2001; Haydock & Koenig, 2002). Rather, empirical tests of skew models suggest that the outcome of reproductive conflict depends on the details of the competition—for example, the cost of producing offspring, the risks of escalated conflict, and the accuracy with which parents can distinguish their own offspring from that of a rival breeder (Cant, 2012).

Happily, the inability of simple models to explain some of the most conspicuous features of cooperative breeding systems has spurred rather than hindered research, and revealed some unexpected and intriguing patterns. For example, studies of cooperative breeding vertebrates have revealed surprising individual consistency in helping effort and the existence of cooperative and less-cooperative "personalities" within groups (Arnold, Owens, & Goldizen, 2005; English, Nakagawa, & Clutton-Brock, 2010; Le Vin, Mable, Taborsky, Heg, & Arnold, 2011). The sources of this consistency and its adaptive significance are topics of much current interest (Bergmuller, Schurch, & Hamilton, 2010; Dingemanse, Kazem, Reale, & Wright, 2010). In cooperative cichlids (Balshine-Earn, Neat, Reid, & Taborsky, 1998; Bergmüller & Taborsky, 2005) and naked mole rats (Reeve, 1992), there is some evidence that dominant individuals use aggression to coerce subordinates to help, but in other cooperative vertebrates coercion and punishment do not appear to be major drivers of variation in helping effort. Acts of aggression and punishment, when they do occur in these systems, usually appear related to conflict over reproduction or social status, rather than over help (Cant, 2012). In female mammals, where offspring are costly to produce in terms of both time and resources, threats of infanticide appear to be effective at suppressing reproduction in subordinates, so that actual acts of infanticide rarely need to be carried out (Cant, 2011; Saltzman, Digby, & Abbott, 2009). Studies of fish size hierarchies and other vertebrate systems raise the intriguing possibility that much of the social behavior we observe is shaped by "hidden" threats, which are triggered only when the social rules they enforce are broken (Cant & Johnstone, 2009). How threats are established and communicated, and how animals "negotiate" a behavioral settlement to conflicts without triggering threats, is another area of active theoretical and empirical interest (Binmore, 2010; Cant & Johnstone, 2009; Hinde, 2006; Lessells & McNamara, 2012).

In parallel with these developments in social conflict theory, the last decade saw rapid progress in theoretical understanding of the role of population structure and demography in social evolution. A large number of models (based on the "infinite island" framework of Wright (1943)) have been developed to explore how features of real populations such as constraints on dispersal (or population "viscosity") and local competition (Irwin & Taylor, 2001; Taylor & Irwin, 2000), aging (Johnstone & Cant, 2010), sex-biased dispersal (Gardner, Arce, & Alpedrinha, 2009; Johnstone & Cant, 2008), and "budding" dispersal (Gardner, 2010; Gardner & West, 2006) influence the strength and direction of selection for "helping" and "harming" traits—that is, traits that increase or decrease, respectively, the fecundity of local group members (reviewed by Lehmann & Rousset, 2010). The models are relevant to social and cooperative vertebrates, which usually live in close-knit groups in which there are severe dispersal constraints and intense local competition for resources and reproduction. To date, however, these models have received little attention from empiricists, possibly because some of the assumptions of infinite island models (e.g. infinite clutch size, infinite numbers of groups, asexuality) appear unrealistic to field researchers. As a consequence, it is unclear how relevant the predictions derived from this framework are for cooperative fish, birds, and mammals, or how observed deviations from the model assumptions should affect the evolution of helping and harming in real systems.

The aim of this article is to draw together over a decade of research on an unusually tractable mammalian cooperative breeder, the banded mongoose (*Mungos mungo*), and evaluate the results of our long-term study against advances in social evolution theory that have occurred over the same period. In particular, we focus on the main conflictual and cooperative features of the social system: first, the often intense forms of reproductive competition apparent among co-breeders of both sexes; and second the conspicuous and unusual forms of helping behavior observed in this system. We discuss ways in which banded mongooses deviate from the assumptions of reproductive skew theory and demographic models of kin selection, and suggest ways where social evolution theory can be made more relevant to real systems. Banded mongooses share many features with meerkats (*Suricata suricatta*), which are well known—thanks to 20 years of research by Tim Clutton-Brock and colleagues—and with dwarf mongooses (*Helogale parvula*) on which pioneering research was carried out in the 1970s and 1980s by Jon Rood, Anne Rasa, Peter Waser, and Scott Creel. However, as the banded mongoose study has progressed and matured, so the distinctions between social systems have become more apparent. These differences between social mongooses are particularly useful to elucidate the ecological causes of intraspecific variation in helping behavior and reproductive skew.

## 2. THE BANDED MONGOOSE STUDY SYSTEM

Banded mongooses are distributed widely across sub-Saharan Africa (Cant & Gilchrist, 2013), and have been studied in detail at sites in northern Botswana (Laver, Ganswindt, Ganswindt, & Alexander, 2012), and the Serengeti (Rood, 1986). However, most of what we know about the banded mongoose's social behavior comes from a long-term study of a population living on and around Mweya Peninsula in the Queen Elizabeth National Park, Uganda (Fig. 6.1). Mweya is a 5 km$^2$ promontory extending into Lake

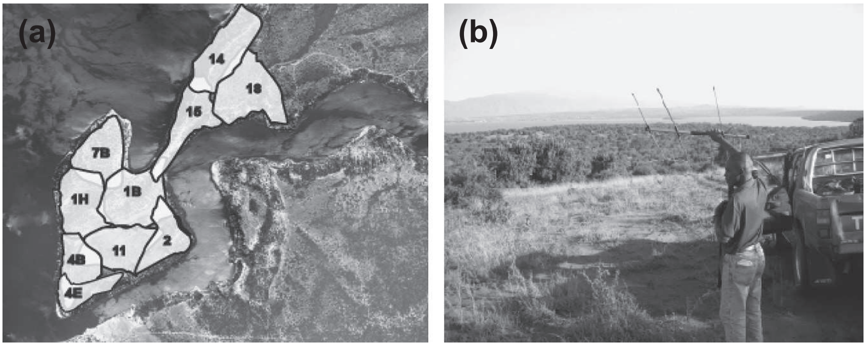

**Figure 6.1** (a) Mweya Peninsula is located on the shores of Lake Edward in western Uganda. The map shows approximate home ranges of banded mongoose groups in November 2012. At any one time the population consists of around 250 individuals living in 10–12 groups. (b) The habitat is scrub-savannah with thickets of *Euphorbia*, *Capparis*, and *Azima*, and is home to populations of buffalo, hippo, elephant, and lion.

Edward and connected to the mainland by a narrow ridge. Mweya village on the peninsula was the site of the former Nuffield Institute for Tropical Ecology in the 1960s (later renamed Uganda Institute of Ecology), which drew researchers from around the world, including Ernest Neal and Jon Rood who made the first detailed observations of banded mongooses in the wild (Neal, 1971; Rood, 1974, 1975). After the political instability of the region in the 1970s and 1980s, Daniela de Luca and Rosie Woodroffe from the Institute of Zoology, London, returned to follow up on Rood's study (De Luca & Ginsberg, 2001). Building on this research, the Banded Mongoose Research Project was started in 1995 by Michael Cant and Tim Clutton-Brock from the University of Cambridge, and continued by a succession of PhD students and postdocs from Cambridge and later the University of Exeter, where the main project is now based. Since 2007, we have brought these data together into a single database spanning 17 years that contains information on >2500 individuals that have lived and died in the population since then. Molecular genetic analysis lead by Hazel Nichols at the University of Cambridge has allowed an in-depth analysis of reproductive success (through genetic parentage assignment; Nichols, Amos, et al., 2012; Nichols, Amos, Cant, Bell, & Hodge, 2010; Nichols, Bell, Hodge, & Cant, 2012) and an understanding of the relatedness structure of the population (Nichols, Jordan, et al., 2012).

At any one time, the study population consists of around 250 individuals living in 10–12 groups (Fig. 6.1). Typically seven groups occupy the peninsula proper, with the remaining groups inhabiting the adjoining mainland. Most of this area is shrub and savannah, dominated by medium-height grassland interspersed with thickets of *Euphorbia candelabrum*, *Azima tetracantha*, and *Capparis tomentosa*. The peninsula is divided into lower and upper halves by a steep grassy fault approximately 40 m high. The lower part of the peninsula is uninhabited by humans but the upper peninsula is the site of a village of approximately 300 people and 100 buildings. The area inside the village is sparsely vegetated and provides some access to the food refuse for the banded mongoose groups whose territories encompass it (Gilchrist, Otali, & Mwanguhya, 2004). The climate is equatorial, with little seasonal fluctuation in temperature or day length. Annual precipitation is typically 800–900 mm, with two dry periods in January–February and June–July (Cant, 2000).

At Mweya, banded mongooses live at relatively high density (mean 18 individuals/km$^2$ (Gilchrist & Otali, 2002) compared to approximately 3 km$^2$ on the Serengeti plains (Waser, Elliott, Creel, & Creel, 1995)), and each group aggressively defends a territory ranging from 0.3 to 2 $km^2$ in area (Cant, 2000; Rood, 1975). Each group sleeps together in one of many dens in their territory, emerging shortly after dawn to commence foraging. Individuals locate their prey by smell, and use their forepaws to dig if necessary. Their diet is mainly insectivorous but they will also eat small vertebrates, eggs, fruit, and human refuse opportunistically (Gilchrist et al., 2004). Most prey items are found in dung, leaf litter, or buried up to a few inches in soil. Although groups forage as cohesive units, usually within 10–20 m of one another, foraging is not a cooperative activity and food items are defended aggressively from others (De Luca & Ginsberg, 2001). Morning foraging sessions last for 3 to 4 h before the hottest part of the day when the group stops to rest in the shade. Foraging begins again in the late afternoon for 2 to 3 h before sunset, when the group retires into a night-time den. Dens are located underground, often in an abandoned termite nest or an erosion gully in a dense thicket of bushes. Dens change regularly, often every two or three days, but some are returned to frequently (Cant, 1998).

## 3. DEMOGRAPHY

### 3.1. Group Composition and Dynamics

The banded mongoose has one of the largest average group sizes of any carnivore (Russell, 2004), with some groups containing as many as 75 adults, although groups of 10–30 are more typical (median = 18 adults, interquartile range = 9.25; Cant, 2000). Groups generally comprise a "core" of breeding adults (1–5 females and 3–7 males) that reproduce 3–4 times per year, alongside a subset of younger individuals that breed occasionally (Cant et al., 2010; Nichols, Amos, et al., 2012; Nichols, Bell, et al., 2012; Nichols, Jordan, et al., 2012). The adult sex ratio of the population is significantly male-biased (mean proportion males per group is 0.62), although this varies between groups and over time (Cant, 2000). Males outnumber females in almost all age classes (Fig. 6.2). The cause of this excess of males is currently unclear, but sex differences in lifespan, dispersal, and sex ratio at birth could all play a part. Reproduction is synchronized within, but not between groups: all adult female group members enter estrus within a week or so of each other, and most females give birth in close synchrony, usually on the same night (see Section 4.1). The resulting mixed litter of up to 23 pups is reared communally, with both parents and nonbreeding group members contributing to pup care (Gilchrist & Russell, 2007).

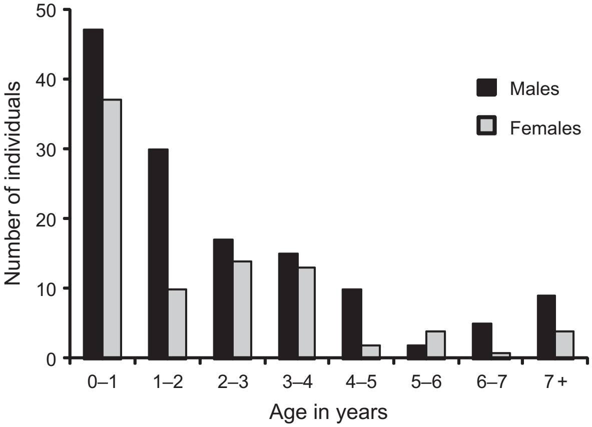

**Figure 6.2** Age composition among 11 groups of the Mweya population as of November 2012. The adult sex ratio is significantly male-biased ($N = 222$, proportion male = 0.62, $\chi^2 = 11.26$, $P < 0.001$).

As with many cooperatively breeding mammals, banded mongoose offspring display a high degree of natal philopatry, and almost all remain in their natal group beyond sexual maturity. However, rather unusually for a cooperative breeder, offspring of both sexes breed in their natal group before dispersal and some may remain as breeders in their natal group for their entire lives (Nichols et al., 2010). Banded mongoose females do not leave their group voluntarily but rather are forcibly evicted by older, socially dominant females (Cant, Otali, & Mwanguhya, 2001). Subordinate females are evicted *en masse*, with up to 16 individuals being evicted at the same time (Cant et al., 2010; Cant et al., 2001). Males are also sometimes evicted and sometimes leave voluntarily, usually when they encounter a dispersing group of evicted females. When subordinates of both sexes are evicted simultaneously, they disperse in separate same-sex cohorts. Dispersing cohorts have been known to travel over 20 km (Cant et al., 2001), but many form territories close to their natal group.

New groups form when a cohort of dispersing males fuses with a cohort of females from a different natal group and establishes a territory. In some cases, both cohorts forming new groups are dispersing "floaters", but cohorts frequently take over existing groups, evicting all same-sex adults in the process. For the 10 new groups that formed in the study area between 1997 and 2009, three were formed by the fusion of single-sex dispersing cohorts. In seven cases, a new group was formed when a cohort of dispersing males (two cases) or females (five cases) displaced same-sex adults present in an existing group. In one further case, a cohort of dispersing females established a territory and bred despite never being permanently joined by any males. Females in this group mated with males from neighboring groups whilst in estrous, however both adult and offspring survival was low and the group dissolved within 24 months.

Once formed, social groups remain stable, and migration between established groups is virtually absent (only three individuals have immigrated into existing groups since 1997). This pattern is similar to that observed in meerkats, where females do not immigrate into established groups, and females are often evicted in cohorts ranging from two to six (mode 4; Stephens, Russell, Young, Sutherland, & Clutton-Brock, 2005). In dwarf mongooses, males and females often emigrate in small groups (in around 60% of dispersal events; Waser, Creel, & Lucas, 1994), and in both meerkats and dwarf mongooses more males than females leave their natal groups. In banded mongooses, a similar (small) percentage of males and females leave their natal groups: since 1997 around 12% of females and 13% of males left their natal group. However, out of this pool of departing individuals, females were twice as likely to succeed in establishing a new group within the study area (see Section 4.5). This may imply that females are more successful at attracting mates and founding new groups, or that males disperse farther than females. On the current evidence, therefore, it appears that successful group founding is female-biased in the banded mongoose. However, we need more information on the fate of dispersing males to know whether this pattern among our limited number of study groups is replicated at the population level.

## 3.2. Intergroup Competition and Sources of Mortality

Banded mongoose groups are highly territorial, with frequent aggressive interactions occurring between groups at territory boundaries (Cant, Otali, & Mwanguhya, 2002; Jordan, Mwanguhya, Kyabulima, Ruedi, & Cant, 2010). Competition occurs between neighboring groups over access to food and space, with larger groups often extending their territories into those of their smaller neighbors (Müller & Manser, 2007). Within the study area, some groups have access to refuse sites that contain high-energy food resources. Individuals in groups occupying these territories were heavier and in better condition than in groups on the more natural territories, and females carried more fetuses (Otali & Gilchrist, 2004). However, reproductive output (measured as number of emerged pups) was not higher in these territories. Pup mortality rates were higher in groups with access to refuse sites, although the difference was only significant for male pups (Otali & Gilchrist, 2004).

Encounters between groups can be extremely hostile, with fights frequently leading to severe injury and even death: intergroup fights are responsible for 8% of adult mortality where cause of death is known (Jordan et al., 2010). When groups have dependent pups, intergroup infanticide is common. Over a 29 month period, studying 10 social groups, Müller and Bell (2009) observed 12 separate occasions of infanticide by neighboring groups, involving the death of 17 pups. During the same study period, Müller and Bell (2009) also observed two kidnapping events, where pups under two weeks old were removed from the den by neighboring groups and carried into their territory, without any signs of aggression. On one of these occasions, the female kidnappers were confirmed to be allolactating and suckling the kidnapped pups, despite not being pregnant or having dependent pups of their own at the time. Müller and Bell (2009) propose that both infanticide and kidnappings are likely to be adaptive and can be explained through the benefits of group augmentation (*sensu* Kokko, Johnstone, & Clutton-Brock, 2001).

Predation and frequent conflicts between neighboring groups take their toll particularly on pups, with less than half surviving to maturity. Young individuals are the most vulnerable, with yearly mortality rates of around 0.7 for pups, 0.22 of subadults and 0.14 for adults (Otali & Gilchrist, 2004). For most individuals the cause of death was not known, illness with visible symptoms or death by "old age" being indicated in only a few cases. The most common known cause of death was predation, with Marabou storks, martial eagles, monitor lizards, and leopards accounting for approximately 35% of confirmed deaths during the 17-year study period. Banded mongooses exhibit a mutualistic grooming relationship with warthogs (a rare example of a mammal–mammal mutualism), which led to deaths in some cases. A few individuals died from aggression from the warthogs, and a few were accidentally squashed while grooming them. Human-related causes of death include 27 individuals that have been hit by vehicles, four animals that received lethal burn injuries while foraging in smoldering rubbish pyres; and three individuals that were electrocuted by faulty wiring in the village.

## 3.3. Relatedness Structure and Inbreeding

The first large-scale investigation into the genetic structure of the Mweya population (Nichols, Jordan, et al., 2012) included 1250 individuals genotyped at 14 microsatellite loci. This study found that the banded mongoose population was highly structured, with relatively strong differentiation among breeding groups considering their close spatial proximity ($F_{ST}$ among groups = 0.129). This was probably due to the high level of natal philopatry (i.e. clustering of relatives), combined with a low level of gene-flow between groups (a lack of immigration and low level of extra-group mating). Although members of neighboring packs have occasionally been observed to mate during intergroup fights (Cant et al., 2002; Jordan et al., 2010), evidence for extensive gene-flow between groups is weak. Groups were no more genetically similar to neighboring groups than nonneighboring groups, and the level of population structuring was high, suggesting a high degree of reproductive isolation between adjacent groups (Nichols, Jordan, et al., 2012).

All banded mongoose groups at our study site contain close relatives, but the relatedness structure of groups changes over time since they were formed (Nichols, Jordan, et al., 2012). In the newly founded groups, females are genetic relatives, males are genetic relatives, but males and females are unrelated (mean relatedness (±SE) between adult males = 0.125 (±0.016), adult females = 0.110 (±0.027), adult males to females = −0.021 (±0.029); Fig. 6.3a). This pattern is concordant with observations of budding dispersal, with males and females originating from different natal groups. Group formation by unrelated pairs almost certainly serves to avoid inbreeding (Cant et al., 2001) and is displayed in other cooperative mammal species such as mole rats (Burland, Bennett, Jarvis, & Faulkes, 2002; Ciszek, 2000). While relatedness between males and females is low in newly formed banded mongoose groups, the accumulation of philopatric offspring and death of founders leads to mean relatedness between opposite-sex adults increasing over time (by 8 years after founding, mean $r$ between male and female breeders = 0.23, versus mean background $r$ between opposite-sex adults of 0.041; Fig. 6.3b). Although the generality of this finding remains to be explored, similar high levels of relatedness have been observed between opposite-sex breeders in naked mole rats, Damaraland mole rats and dwarf mongooses, where individuals often inherit breeding positions in their natal group (Burland et al., 2002; Keane, Creel, & Waser, 1996; Reeve, Westneat, Noon, Sherman, & Aquadro, 1990). However, this pattern seems unlikely to occur in the majority of cooperative breeders, where immigrants are accepted or groups dissolve on the death of group-founders (Haydock & Koenig, 2002).

While the presence of closely related opposite-sex breeders in older groups might be expected to lead to incest, molecular genetic analyses

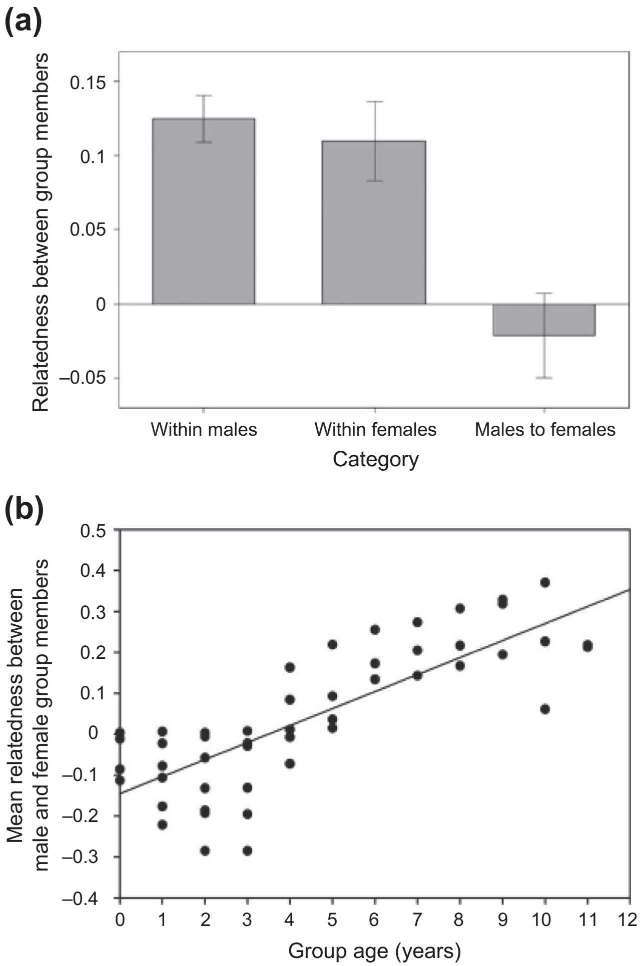

**Figure 6.3** Patterns of genetic relatedness in banded mongoose groups. (a) Relatedness within and between sexes in newly established groups. (b) Relatedness between sexually mature male and female group members (adults over 2 years old) over time since groups were founded. The graph shows mean values per group-year and a linear regression fitted to the data. Data are from 1250 banded mongooses living in 14 groups between 2000 and 2009 (Nichols, Jordan, et al., 2012).

(Nichols, Jordan, et al., 2012) showed little evidence of close, frequent inbreeding. There is no relationship between mean adult relatedness and mean pup homozygosity, suggesting that inbreeding is avoided even in established groups. In many social mammals, inbreeding is avoided through the dispersal of one sex prior to breeding (Clutton-Brock, 1989).

Generally, females disperse from their group when the likely tenure of their fathers exceeds their age of first breeding (Clutton-Brock 1989; Lukas & Clutton-Brock, 2012). However, the banded mongoose is an exception to this rule; male group founders live up to 9 years after the formation of groups, while natal females begin to breed at ~1 year old despite the likely presence of their father, brothers, and other close male relatives (Cant, 2000). In other species where close male relatives of a breeding female are present, extra-group paternity is often used as a means to avoid inbreeding e.g. in pilot whales (Amos, 1993) and fairy wrens (Brouwer, Van de Pol, Atema, & Cockburn, 2011). As described, while extra-group matings do occur in the banded mongoose, they appear to be rare (Jordan et al., 2010) and the resulting gene-flow between groups is not extensive enough to undermine population structure (Nichols, Jordan et al., 2012). The extent to which the banded mongooses avoid inbreeding, and the mechanisms that they employ to do so, is a focus of current research.

## 4. REPRODUCTIVE CONFLICT

### 4.1. Patterns of Female Reproduction

One of the reasons banded mongooses have attracted so much research interest is that most females in each group give birth together in each breeding attempt (Hodge, Bell, Gilchrist, & Cant, 2011; Rood, 1975). This low degree of "reproductive skew" among females contrasts with the typical high skew pattern exhibited by other social mongooses such as meerkats, (Clutton-Brock et al., 2001; Clutton-Brock, Hodge, Flower, Spong, & Young, 2010), dwarf mongooses (Keane et al., 1996), and yellow mongooses (Solomon & French, 1997; Vidya, Balmforth, Le Roux, & Cherry, 2009). Typically all adult females enter estrous 7–10 days after the birth of the previous litter, and mate within a week of one another. Over 80% of females in each group conceive in each breeding event, and almost all pregnant females (93%) carry their litter to term (Cant et al., 2010; Gilchrist et al., 2004). On average, four females give birth in any given breeding event, with a range of 1–12. In 63% of cases, all the pregnant females in a group give birth on the same morning (Hodge et al., 2011; Fig. 6.4a). On one occasion 12 females synchronized birth to the same day in this way. In the remaining "asynchronous" breeding attempts (i.e. those where females give birth on different days) all females give birth within 1–30 days of one another. Pups are guarded in an underground den for the first c. 4 weeks of life, after which they start to join the group on foraging trips, becoming nutritionally independent by 3 months old.

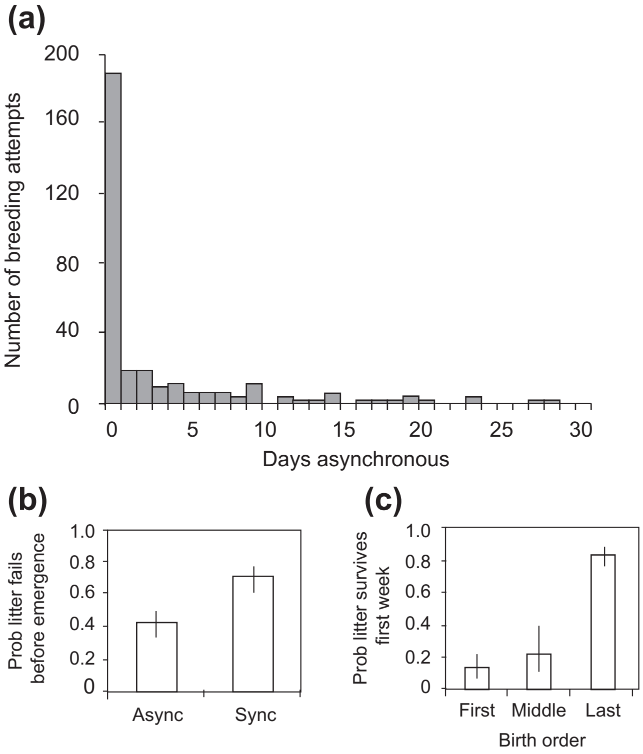

**Figure 6.4** Extreme birth synchrony and pup mortality. (a) Frequency histogram of synchronous and asynchronous breeding attempts. Females give birth on the same day in 63% of breeding attempts. (b) Synchronous communal litters are less likely to fail in the den. (c) In those litters that are asynchronous, females that give birth first are very likely to fail in the first week compared to those that give birth last. This dependency of early pup survival on the pregnancy status of co-breeders is a signature of infanticide. Extreme birth synchrony in this species appears to be adaptation to avoid infanticide and minimize competitive disparities between young. *(Reproduced with permission from Hodge et al. (2011)).*

This unusual plural breeding system raises two key questions: first, why is there such low reproductive skew among female banded mongooses; and second, why do female group mates exhibit such a remarkable degree of birth synchrony? On one level the answer to the first question is simple: females typically co-breed because individual female reproductive success is maximized when 3–5 females breed together, and litters in which there is only a single female breeder fare particularly badly (Fig. 6.5a). But this just pushes the question one step further back: why is the survivorship of single-female litters so poor? One possibility is that singly breeding females

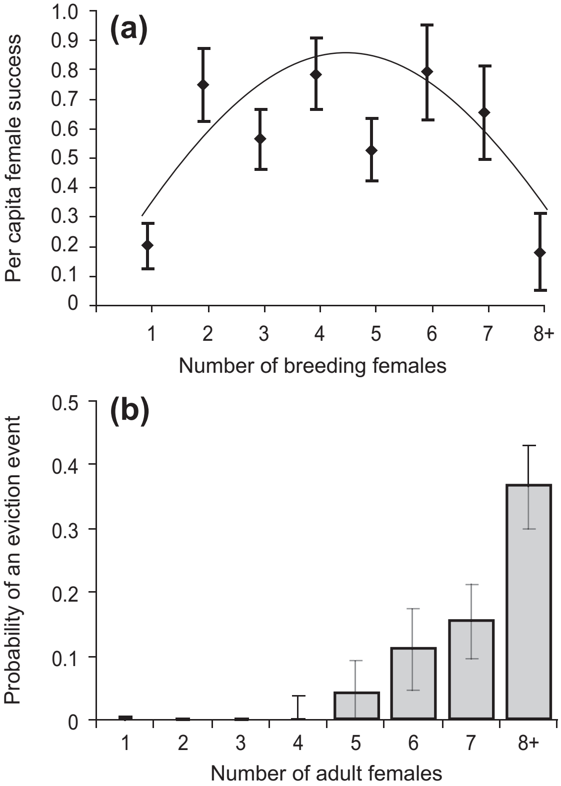

**Figure 6.5** Reproductive conflict and eviction. (a) Female-reproductive success (per capita number of pups surviving to nutritional independence) as a function of the number of females that gave birth. Data are from 306 breeding attempts in 19 groups (Cant et al., 2010). The poor success of females that breed singly appears to be the result of the within-group infanticide. At the other end of the scale, the poor success of females when eight or more females reflects competition for food in large litters. (b) Probability of a mass female eviction event as a function of the number of females that gave birth. Data are from 226 breeding attempts in 15 groups. Older, socially dominant females respond to reproductive competition from subordinates by evicting groups of subordinate females, but subordinate females do not exercise reproductive restraint when there is a high risk of an eviction event.

do badly because of the responses of other group members: perhaps other group members kill or fail to care for litters when only a single female breeds. However, a plausible alternative is that when conditions are very poor, only the female in the very best condition can manage to produce young. In other words, the difference in offspring survival between single- and multiple-female litters might not reflect a causal relationship but instead could be due to variation in a third factor, such as food availability.

Recently, we carried out an experiment to establish the causality of this pattern by "switching off" breeding females using a short-acting contraceptive (Cant et al., in preparation). For eight breeding attempts, we suppressed reproduction in all except a single dominant female and compared patterns of early-life care and pup survival when this female reproduced alone compared to unmanipulated breeding attempts in the same group before and after the contraceptive treatment. All eight single-female litters failed in the first few days after birth, whereas the control litters never failed in this period. The spike in the early-life litter failure in treatment breeding attempts was not due to a lack of care: there was no difference between treatment and control litters in the number of babysitters left behind during foraging trips, nor the frequency with which the group returned to the natal den to feed offspring. Rather, our data suggest that treatment litters died because they were killed by other members in the group, possibly one of the several older dominant females that had been treated with the contraceptive. Data from asynchronous litters lend support to this interpretation and suggest that within-group infanticide is common when females give birth on different days. These asynchronous litters have lower survival to emergence from the den (Fig. 6.4b). Pups that are born first almost never survive the first week of life, whereas the offspring of females that give birth last have very high survival in the first week (Hodge et al., 2011; Fig. 6.4c). The dependency of early life pup survival on the pregnancy status of other group females is a signature of within-group infanticide as a main source of litter mortality (Young et al., 2006; Young & Clutton-Brock, 2006).

Together our experiment and natural observations suggest that females kill litters when these are certain not to contain their own offspring. Monopolization of reproduction is counterproductive in these circumstances because it leaves offspring vulnerable to infanticide. Moreover, from Fig. 6.5a, it is clear that banded mongoose groups are capable of rearing many more young than a single female can produce, so a putative dominant female suffers little cost when 1–6 females breed alongside her, and hence has little to gain from suppressing reproduction in other females. In meerkats and dwarf mongooses, which live in smaller groups and drier habitats, additional co-breeders inflict substantial costs on the reproductive success of dominants, and there is much more to be gained from monopolizing the reproduction (Clutton-Brock et al., 2010; Creel & Waser, 1991). Variation in the cost of co-breeding (i.e. the "costly young" model; Cant & Johnstone, 1999) may offer the best explanation for cross-species variation in the female reproductive skew in the social mongooses.

Selection to avoid infanticide also helps to explain why females synchronize birth to the same day. Any female that gave birth earlier than the others would likely have her pups killed, because in this case clear cues to maternity exist. Discriminating maternity is likely to be more difficult when up to 12 females give birth on the same morning in the same underground den. But giving birth later than other females also involves costs. Newborn pups grow and develop rapidly in the first few days after birth, so females that give birth too late risk producing offspring that are roundly outcompeted by older littermates. These costs of giving birth too soon, or too late, appear to have driven the evolution of extreme birth synchrony in this species (Hodge et al., 2011).

While all females usually give birth on the same day, they typically mate on different days. Older females in the group are usually guarded and mated by dominant males several days before younger females (Cant, 2000). These dominant male "mate guards" follow females around at a distance of <0.5 m all day long during peak estrous, chasing off any other males that come close or attempt to mate. Since birth is usually synchronous, the late-mating females appear to give birth prematurely relative to their co-breeders. The costs of this reduced gestation to individual pups may be offset to some degree because younger females also gestate smaller litters (on average 3.11 ± 0.17 young, compared to 3.53 ± 0.11 in older females). Nevertheless, genetic analyses show that older females produce more surviving offspring than younger females, particularly when food is scarce (Nichols, Bell, et al., 2012). Older, dominant females are buffered against environmental fluctuations and breed all year round, whereas younger females typically breed only when food is sufficiently abundant (Fig. 6.6). Skew in the banded mongooses is low compared to meerkats and dwarf mongooses, but older females do still obtain a disproportionate share of the reproductive output of the group. Thus our molecular genetic research shows is not a truly "egalitarian" breeding system, and that the degree of reproductive skew among females fluctuates with group composition and resource availability.

## 4.2. Reproductive Control via Eviction

Figure 6.5a shows that individual female-reproductive success remains high even where six or seven females reproduce together. Groups can easily raise more young than a single female can give birth to, and for pups there is safety in numbers. However, as the number of breeders grows large individual reproductive success starts to decline, and is very low when eight or more females reproduce. This decline appears to be driven by competition

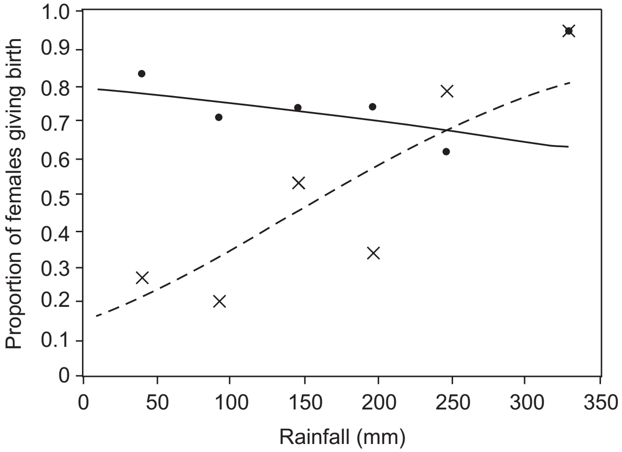

**Figure 6.6** The relationship between rainfall and the proportion of females giving birth. Solid line: oldest female in each group; dashed line: fifth oldest female in each group. The graph shows the regression and predicted means from a Generalized Linear Mixed Model (GLMM) fitted to data from 97 breeding attempts (Nichols, Bell, et al., 2012).

among foraging pups: pup survival from emergence to nutritional independence decreases with increasing litter size (Cant et al., 2010). Competition arises because ephemeral insect food resources are likely to be more rapidly depleted by very large litters, and because pups compete for a limited number of helpers.

In most cooperative mammals, dominant females respond to reproductive competition by suppressing the reproduction of female subordinates. Theory suggests that this can be achieved through brute force (e.g. aggression or infanticide) or through the use of threats of eviction or infanticide (Cant, 2011). For example, the "restraint" model (Johnstone & Cant, 1999) suggests that dominants can use the threat of eviction to deter subordinates from producing offspring. This model is based on three assumptions: (1) that subordinate reproduction is costly to dominant females; (2) that dominant females respond to reproductive competition from subordinates by evicting subordinate breeders; and (3) that subordinate females respond to the threat of eviction by exercising reproductive restraint. We found strong support for the first two of these assumptions. Dominant females suffer costs when large numbers of subordinates reproduce (Fig. 6.5a) and respond by evicting females en masse (Fig. 6.5b). Evictions often last for days, and involve high levels of aggression and violent targeted attacks. On average, six females are evicted per "eviction event".

As in meerkats (Young et al., 2006), evicted females often spontaneously abort their litters, most likely as a causal response to the stress of attack and exclusion from the group. Females are more likely to be targeted if they are pregnant, and more likely to be accepted back in the group if they abort the litter, suggesting that dominant females can use eviction as a means to reduce reproductive competition in the current litter (Cant et al., 2010).

However, we found no support for the third assumption of the restraint model. Subordinate females are not less likely to breed when there is a high probability of eviction, indicating that the threat of eviction is not effective at deterring subordinate reproduction (Cant et al., 2010). Eviction threats are ineffective in this case because evicted females can abort their litter and often regain entry to the group, rendering preemptive restraint unnecessary. In addition, exercising restraint does not offer full protection against eviction, since even nonreproductive females (and males, see below) were frequently evicted, possibly owing to dominants' inability to target pregnant females with complete accuracy. In general, threats are expected to be less effective in multimember groups where transgressors cannot be identified with certainty, compared to two-player situations where subordinates are certain to suffer the consequences if they fail to exercise reproductive restraint (Cant, 2011; Cant et al., 2010). The conclusion is that dominant females use eviction to limit reproductive competition, but the *threat* of eviction is not effective at suppressing subordinates. In general, we expect threats of infanticide to be much more effective than threats of eviction in enforcing reproductive suppression in cooperative mammals (Cant, 2011).

## 4.3. Reproductive Competition among Males

In stark contrast to females, reproductive skew among males is high and males compete aggressively to mate with estrous females. Although females enter estrous within a week of one another, at any one time two or three high ranking "mate guarding" males monopolize access to females in peak estrous. Mate-guarding males are significantly heavier and older than average, and obtain 83% of observed matings (Cant, 2000). Genetic analysis shows that 85% of paternity is assigned to the three oldest males in each group (Nichols et al., 2010; Fig. 6.7). Younger males also engage in mate-guarding behavior, but achieve low reproductive success because they mate guard fewer females, and less successful females, than older males in the same group. A second reproductive strategy adopted by males is called "pestering": pestering males follow female-mate guarded pairs at a short distance (c. 5 m), waiting for any opportunity to sneak a mating with

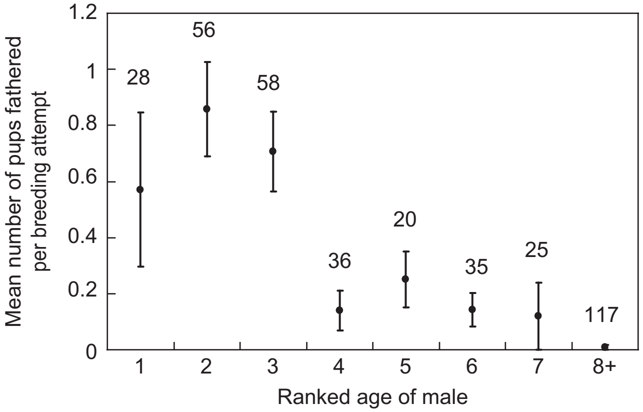

**Figure 6.7** Male-reproductive success (number of surviving pups fathered per successful breeding attempt) as a function of male age rank within groups (oldest male = rank 1). Data are from 90 males from five groups in 44 breeding attempts (Nichols et al., 2010). Successful breeding attempts are those in which at least one pup survived to emergence. Older males monopolize paternity because they mate-guard older females, who produce more surviving pups.

females, as arises, for example if the mate-guarding male stops to handle and eat a particularly large or tasty food item, such as a dung beetle. Females, for their part, often go to some lengths to escape from their mate guards and mate with pestering males. Over half of females are observed to mate with a male other than their mate guard during estrous, usually surreptitiously or in dense undergrowth, suggesting that multiple mating is quite common. These multiple matings translate into shared paternity in 23% of litters (Nichols et al., 2010), indicating that pestering males do sometimes succeed in fathering offspring, although they are much less successful than mate-guarding males.

The observed distribution of paternity appears to be a compromise between the interests of mate-guarding males and estrous females. Mate guards gain obvious benefits from attempting to monopolize paternity. Females may gain genetic benefits from multiple mating because this allows them to mate with more compatible, or less related males, or because they can exploit sperm competition to ensure that they are fertilized by the most competitive and fertile males. Inbreeding avoidance may be particularly important in banded mongooses because offspring remain in their natal group long-past maturity, and potential mates include both nonrelatives and closely related individuals. Another possibility is that females mate with multiple males to increase paternal investment (Cant & Reeve, 2002;

Harada & Iwasa, 1996; Houston, Gasson, & McNamara, 1997) as shown in dunnocks *Prunella modularis* (Davies, Hartley, Hatchwell, & Langmore, 1996) and cichlids *Julidochromis transcriptus* (Kohda et al., 2009). This is a plausible driver of polyandrous mating in the banded mongoose because males invest highly in pup care and there is evidence that males who are likely to have fathered pups in the communal litter increase their levels of help (Gilchrist & Russell, 2007; Section 5.1).

## 4.4. Eviction of Males

In 64% (32 out of 50) of eviction events, only females were evicted. In the remaining 36% of cases males were also evicted along with females. While 30% of evicted individuals are male, there have been no cases of male-only evictions. Males are attacked and evicted by other males, and by attacks from mixed sex groups of males and females (Cant et al., 2001). The triggers of male evictions are poorly understood at present. Unlike the case for females, reproductive conflict does not seem to be the cause of male evictions: the number of adult males in the group is not a predictor of male eviction and both young and older males are targeted. Moreover, given that the oldest males in the group dominate paternity, subordinates males (unlike subordinate females) do not inflict reproductive costs on dominants. One possibility is that recorded cases of male eviction actually represent voluntary departure from the group, co-occurring with forcible eviction of females. However, it is not clear why subordinate males would stand to gain from dispersing at the same time as female group mates: in the 18 eviction events that involved both sexes, evicted males and females split into same sex groups and went separate ways within days of leaving the group.

## 4.5. Dispersal and Population Consequences of Eviction

Over the 18-year study, a total of 105 males and 160 females were evicted from their natal group at least once. Approximately half of the evicted males (52%) and one fifth (18%) of the evicted females dispersed away from the study area, and were not observed again in the study population. Among those adults that were evicted, 13% of males and 27% of the females established a new group within the study area, and around 30% of both sexes were later admitted back to their natal group. A further 8% of evictees sustained deadly injuries either during or soon after the eviction in clashes between the new splinter groups and established groups.

Noticeably, while females were evicted at a higher rate than males, their evictions also incurred more violence and in evictions where both sexes were chased away, females tended to sustain the most injuries, with males coming off relatively unscathed (S. Hodge, personal observation). Males were also observed (101 cases in total) to voluntarily leave their natal group, often in pursuit of estrous females from neighboring groups. In 60% of these 101 cases, the "roving" males joined a coalition of evicted females, or joined an existing group; 30% of these voluntary roving trips resulted in the males returning to their old pack, and in a few cases the males dispersed off the study area. In contrast, 12 females were observed to join an existing group without obvious preceding violence from their pack members. but observations were limited, and these cases could also have been evictions.

Eviction is the main driver of gene-flow in this population of banded mongooses (Nichols, Jordan, et al., 2012). Evicted groups of females perturb the stability of other groups because they represent a breeding opportunity for low-ranking males who are otherwise excluded from reproduction. In the Uganda population, the attractiveness of dispersing females to males is further amplified by the differential survival of males and females and the consequent male-biased sex ratio among adults. This differential survival may itself arise from sex differences in reproductive skew in males and females. Unlike most long-lived mammals, our preliminary data indicate that males live substantially longer than females in this species (Vitikainen et al., in preparation). Our working hypothesis is that this pattern arises because all adult females in each group breed regularly from the age of one year, whereas males exhibit a dominance hierarchy in which the oldest 1–3 individuals monopolize breeding (Fig. 6.4), and young males must queue for several years to achieve dominant status. In these circumstances, evolutionary queuing models (e.g. Cant & Field, 2001) suggest that nonbreeding males will allocate a greater fraction of resources to survival and somatic repair compared to breeding females of the same age, with the consequence that females should undergo earlier or more rapid senescence than males. We are currently testing this hypothesis.

## 4.6. The Evolution of Reproductive Skew in Banded Mongooses

Theoretical models to explain variation in reproductive skew within and between species diversified rapidly in the last 20 years, but these can generally be divided into two classes. Transactional models assume that skew is determined by threats to breakup the group (by dispersal or eviction). In these models the level of sharing among group members is assumed to be sensitive to the value of dispersal options outside the group. By contrast, incomplete control models assume that dispersal options outside the group are irrelevant and all group members can exert partial, costly control over the distribution of direct fitness. Our results lend no support for transactional models based on either the threat of eviction or dispersal as explanations for reproductive skew in either sex. We have never observed females to disperse voluntarily, even when experimentally suppressed using contraceptives (Cant et al., in preparation). It is therefore unlikely that subordinates are permitted to breed by dominants to induce them to stay in the group, as early transactional models assumed (e.g. Vehrencamp, 1983)—nor do subordinate females exercise reproductive restraint to avert the threat of eviction (Cant et al., 2010). Groups are not in the steady state assumed by transactional models; rather, our results suggest a more dynamic system in which subordinates escape from infanticide by synchronizing reproduction with dominants, restricting dominant females to using eviction as the primary means of limiting the level of reproductive competition faced by their pups. Since dominant discrimination of pregnant versus nonpregnant females is not perfect, preemptive restraint to avoid eviction is unlikely to be an evolutionarily stable strategy (Cant et al., 2010). Subordinate females take their chances, and the result is the frequent eviction of large numbers of dispersing propagules. By contrast in systems where eviction threats are effective (e.g. fish size hierarchies; Ang & Manica, 2010, Buston, 2003; Buston & Cant 2006), dominants rarely need to exercise the threat and consequently dispersal among adults is rare or nonexistent. The conclusion is that the way in which the within-group conflict is resolved has important consequences for population dispersal and structure, and intergroup competition. These population level consequences of within-group conflicts at different levels of biological organization remain little explored to date.

Among males, dominants maintain their reproductive monopoly and social rank through acts of aggression, as is common in primate social systems (Port & Kappeler, 2010). In banded mongooses, male–male aggression is usually restricted to estrous periods, although we have observed more subtle dominance interactions among males outside of mating periods. There is no evidence that the distribution of paternity reflects reproductive transactions to avoid group breakup. The high skew among males, despite low skew among females, arises for two reasons: (1) because females do not enter peak estrus on exactly the same days, allowing the same dominant males to guard multiple females in a single estrus; and (2) because dominant males choose to mate guard older, more successful females (Nichols et al., 2010).

# 5. HELPING BEHAVIOR

## 5.1. Babysitting and Escorting

Banded mongooses exhibit two main forms of helping behavior: "babysitting" and "escorting". Most group members over 6-months old help to rear the communal litter and engage in one or both of these activities (Cant, 2003; Gilchrist, 2004; Gilchrist & Russell, 2007). Babysitting refers to the behavior of subadults and adults that remain at the underground den to guard young pups from predators and rival mongoose groups. During this period pup nutrition comes from milk and pups appear to be suckled indiscriminately (Cant, 2003; Gilchrist, 2006; Gilchrist et al., 2004; Neal, 1971; Rood, 1975). Approximately 4 weeks after birth, pups emerge from the den and begin foraging with the group. For the first 3–5 days after emergence, pups approach and follow potential helpers, begging for food. Competition between pups for the best helpers is initially intense (Hodge et al., 2009) but after a few days, most pups settle down into an exclusive one-to-one caring relationship with a particular helper. We call this relationship "escorting" and refer to adults that engage in this behavior as "escorts" (Fig. 6.8). Escorts stay close to their associated pup and feed,

**Figure 6.8** Escorting behavior is a unique feature of the banded mongoose system. After spending the first month of life underground, pups emerge from the den and accompany the rest of the group on daytime-foraging trips. During this many pups form exclusive one-to-one caring relationships with particular adult helpers, known as "escorts", who protect, provision, carry, and groom the pup in their care. *(Photo courtesy of Mark Macewan).*

groom, carry, and protect them from predators. By contrast adult-group members that do not become escorts provide very little pup care (Bell, 2007; Gilchrist, 2004). This form of one-to-one helping relationship is to our knowledge unique in cooperative vertebrates. The pup–escort association seems to be initiated primarily by the pup, which defends a "mobile territory" around his or her escort, aggressively repelling littermates if they approach (Gilchrist, 2008; Hodge et al., 2009). However, after a few weeks, escorts also actively contribute to maintaining the pup–adult bond. Experiments have shown that escorts are able to recognize their pups visually and acoustically, and actively bias care toward them (Gilchrist, Otali, & Mwanghuya, 2008).

Males contribute a disproportionate amount to both forms of helping (Cant, 2003; Hodge, 2007). Nichols, Amos, et al. (2012) found that individual males spend a mean of 14.2% of days babysitting per litter, compared to 8.3% in females. Almost half (47.3%) of males escort a pup in any given litter, compared to 37.1% of females. Subordinate males contribute more to babysitting than do breeding females and dominant males (Cant, 2003). In all 25 litters observed by Nichols, Amos, et al. (2012) the top babysitter was male and had no genetically assigned pups in the litters they helped. Babysitting usually overlaps with estrus, so males that have a high probability of mating have more to lose by remaining at the den during this period. Escorting, on the other hand, usually occurs several weeks after estrus has finished, so there is less immediate conflict between helping and breeding activities for this form of care. Both breeding and nonbreeding males and females contribute to escorting, but females that have given birth, and the males that mate-guarded them when the litter was conceived, generally contribute more to escorting than nonbreeders (Gilchrist & Russell, 2007; Section 5.3). Juveniles (under 12 months old) and nonbreeding females are least likely to help, but their contribution to the offspring care (both babysitting and escorting) increases when food is abundant (Nichols, Amos, et al., 2012).

## 5.2. The Costs of Helping

Variation between group members in their relative contributions to offspring care are common in cooperatively breeding species and are often interpreted as the result of a tradeoff between the (direct) fitness costs and the (direct or indirect) fitness benefits of helping (Cant & Field, 2001; Heinsohn & Legge, 1999). Helping is associated with a short-term cost in the banded mongoose; those who contribute highly to help lose weight over the pup-dependent period (Hodge, 2007). Weight is a predictor of reproductive success in this species, particularly for females. Females that are heavier at conception produce heavier emergent pups, suggestive of maternal effects on development (Fig. 6.9). Even short-term weight loss is likely to have negative impacts on the lifetime fitness (Hodge, 2007; Hodge et al., 2009). The magnitude of these weight-loss impacts on long-term fitness differ for different demographic classes of individuals (Bell, Nichols, et al. 2012). For example, younger individuals that are still growing have high-energy requirements and may suffer higher long-term costs from babysitting than older individuals. This may explain why contributions to care are generally low for the juvenile-banded mongooses, and many other cooperative vertebrates. Juvenile meerkats, for example, contribute less to pup feeding, babysitting, digging, teaching, and sentinel behavior than older group members (Clutton-Brock et al., 2000; Thornton & Malapert, 2009). Juvenile white-winged choughs, acquire less food and help at lower rates than adults (Heinsohn & Cockburn, 1994; Heinsohn, 1991); similar patterns are seen in white-throated Magpie-Jays (Langen & Vehrencamp, 1999).

Differences in the fitness costs of care may also explain why males contribute most to offspring care in this species. While both male and female

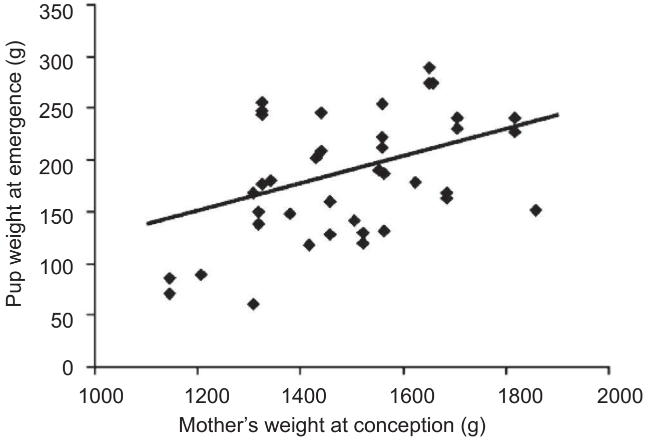

**Figure 6.9** The influence of mother's weight at conception on the weight of pups when they first emerge from the natal den. Data shown are for 39 pups for which maternity was assigned using microsatellite analysis (Hodge et al., 2009). Babysitting periods usually overlap with the time of conception, so investment by mothers in babysitting for one litter may have negative impacts on their reproductive success in the next litter.

helpers lose weight during the pup-care period, the long-term impact of weight loss is likely to differ between the sexes. Among females, body condition influences a number of traits associated with fitness, such as age at first conception (Gilchrist et al., 2004), pup weight (Hodge et al., 2009), and their probability of being evicted from the group (Bell, Nichols, Gilchrist, Cant, & Hodge, 2012). Even short-term reductions in body weight may be costly for females as the helping period often coincides with conception and gestation of the next litter, and weight loss at this time is likely to reduce their probability of breeding successfully (Hodge et al., 2009; Fig. 6.9). Accordingly, experiments show that the female-helping effort is more sensitive to energetic costs than is the male-helping effort (Bell, 2010). For males, on the other hand, there is little evidence that reproductive success or the probability of eviction is related to body condition (Bell et al., 2012; Nichols et al., 2010). The strict dominance hierarchy among males means that subordinate males rarely gain access to estrous females regardless of their body weight (Hodge, 2007), so temporary weight loss is unlikely to have a large impact on the breeding success of these males, explaining why males help at higher rates. This is an example where the different outcomes of reproductive conflict among males and among females can have an impact on sex-specific cooperative effort.

## 5.3. The Benefits of Helping

Other things being equal, helpers are predicted to be more likely to help, and to work harder, when offspring are close relatives (Emlen, 1991; Griffin & West, 2003; Hamilton, 1964). This possibility has been difficult to test in the banded mongoose because their polygynandrous-mating system and low genetic diversity make it difficult to disentangle relatedness from parentage (Nichols, Amos, et al., 2012). However, individuals that are likely to be parents of one or more pups in the communal litter (females that have given birth recently and their male-mate guards) generally contribute more to pup care than those that are less likely to have offspring in the litter (Gilchrist & Russell, 2007). While parents may be more likely to help than nonparents, current studies provide little evidence that genetic relatedness plays a significant part in determining whether or not nonparents help. For example, top babysitters were no more closely related to the communal litter than other adults in the group (mean $r$ of top helpers to litter = 0.25 ± 0.04, mean $r$ of other adults to litter = 0.26 ± 0.02; Nichols, Amos, et al., 2012).

Although parents are more likely to become an escort than nonparents, parents seem unable to identify or direct care toward their own pups (Nichols, Amos, et al., 2012). For example, lactating females suckle pups indiscriminately, and female breeders are no more likely to escort their own pup than the pup of another female (Nichols, Amos, et al., 2012). This is probably due to the high degree of birth synchrony found within groups scrambling cues to maternity and preventing females from identifying their own pups (Hodge et al., 2011). It seems likely that birth synchrony combined with a promiscuous mating system may also prevent other close relatives (e.g. siblings) from recognizing one another based on familiarity, and hence from directing care toward close kin.

In addition to improving the reproductive success of relatives, there may be direct fitness benefits of providing help—for example through group augmentation (Kokko et al., 2001) or because helping increases the probability of securing a mating partner in the future (Reyer, 1986). In the banded mongoose, males do not appear to use helping as a signal of quality to advertise to potential mates because males who provide large amounts of help rarely gain paternity in the subsequent litter (Nichols, Amos, et al., 2012). However, there are potential direct fitness benefits of helping through group augmentation. Where individuals benefit from living in a larger group helpers may directly benefit from raising additional recruits to their group (Kokko et al., 2001). The benefits of group augmentation have been shown to be an important determinant of helping behavior in some cooperative birds (e.g. Kingma, Hall, Arriero, & Peters, 2010), and may explain why meerkats that immigrate into a new group provide care for pups to whom they are not related (Clutton-Brock et al., 2000). Group augmentation may be particularly important in the banded mongoose because large groups often extend their territories into those of smaller neighboring groups, and small groups are particularly vulnerable to intraspecific infanticide.

For the banded mongooses to gain fitness through group augmentation and/or helping kin, the recipients of help must benefit from the care they receive. In other words, pup care should enhance offspring survival and/or future fecundity. Studying the benefits of help in the banded mongoose has an advantage over many other species as the escorting system means that pups vary in the amount of care they receive, even within the same litter. By studying differences in pups within litters, we can therefore be sure that it is the amount of care per se that impacts on pups, rather than some correlate such as territory quality (Hodge, 2005). As is the case with many other cooperatively breeding species (Emlen, 1991), banded mongoose offspring do benefit from the alloparental care that they receive. For example, pup survival increases with average number of babysitters guarding them (Cant, 2003). Pups that spend more time with an escort are fed more, grow faster, and have a higher probability of survival than those that spend less time with an escort (Hodge, 2005). The benefits of early-life care extend into adulthood. High growth during the escorting period reduces the age at which females first breed, so can affect future fecundity (Hodge, 2005).

## 5.4. The Evolution of Cooperative Care in the Banded Mongoose

A recent comparative analysis of mammalian societies suggests that cooperative breeding mammals evolved from monogamous ancestors (Lukas & Clutton-Brock, 2012). As in birds and eusocial insects, monogamy sets the stage for cooperative breeding because relatedness between helpers and offspring is higher under monogamy than polygyny or polygynandry. Lukas & Clutton-Brock adopt a definition of cooperative breeding which explicitly excludes the banded mongooses on the grounds that most adult females breed regularly. This criterion for cooperative breeding has the unfortunate consequence of separating banded mongooses (which are classed as "communal breeders" by Lukas & Clutton Brock) from dwarf mongooses and meerkats, despite the similarities between these systems and strong morphological, chromosomal, and molecular genetic evidence that all the three evolved from a cooperative common ancestor (Veron, Colyn, Dunham, Taylor, & Gaubert, 2004). Crespi and Yanega (1995) argue that classifications of social systems should be *nonarbitrary* (categorizing societies by meaningful features), *universal* (applying to all species), and *evolutionarily informative* (indicative of differences in the way that natural selection acts on social behavior). While a definition of cooperative breeding based on female reproductive skew satisfies the first two features, it is arguably not evolutionarily informative because it ignores the most salient common feature of these social mongoose systems, the fact that they exhibit striking and very similar patterns of cooperative alloparental care.

Monogamy and consequent high genetic relatedness of helpers and offspring may promote the evolutionary transition to cooperative breeding, but our data show that monogamy is not required for the maintenance of cooperative breeding in the banded mongooses (Nichols, Jordan et al. 2012). Selection for helping appears to be maintained by a combination of indirect and direct fitness benefits. Helpers boost the survival of genetically related offspring who may remain as breeders in the natal territory, or disperse as members of a coalition to found new groups in the population. This pattern of budding dispersal can offset some of the local competition costs of helping because it decouples the positive and negative consequences of helping: additional offspring raised as a consequence of cooperation are able to disperse away from their parents, and so avoid competing with them, but still form groups within which relatedness is high (Gardner & West, 2006). In addition to the kin-selected benefits of helping, it is likely that there are substantial direct fitness benefits of helping in the banded mongooses, particularly in relatively small groups that are vulnerable to predation and intergroup competition. Our future work aims to quantify the relative magnitude of direct fitness versus indirect fitness benefits of helping, and to test whether variation in the future direct-fitness benefits of helping explains variation in helping effort.

The (tentative) pattern of female-biased dispersal coupled with male-biased care in the banded mongooses is consistent with the prediction of demographic kin selection models (Johnstone & Cant, 2008). In these models, members of the nondispersing sex are selected to help (i.e. to boost the fecundity of local breeders of the same sex) while members of the dispersing sex are often selected to engage in harming behavior (i.e. to reduce the fecundity of local breeders of the same sex). This is because members of the nondispersing sex are more closely related to local offspring, but suffer the same average level of kin competition as do members of the dispersing sex. In dwarf mongooses and meerkats, dispersal is male-biased, and females provide most of the help—again as predicted by the models. At a broader scale, in cooperatively breeding birds dispersal is typically female-biased and males provide most help (Cockburn, 1998), whereas in most cooperatively breeding mammals dispersal is male-biased and females contribute most to helping (Russell, 2004). It has been argued that individuals of the philopatric sex may help more because they have a greater chance of inheriting a breeding position in future and enjoying group augmentation benefits. However, even in the absence of these future direct fitness effects, the new demographic kin selection models predict that sex differences in dispersal will affect the evolution of life history and behavioral traits that affect other local group members, including helping, infanticide, and aggression (Johnstone & Cant, 2008); and also how the strength of kin selection changes across the lifespan in relatively long-lived species (Johnstone & Cant, 2010). Testing of these "kinship dynamics" models is at an early stage (e.g. see Foster et al., 2012), but they represent an important step in explaining variation in behavior, mortality, and fertility schedules in long-lived social and cooperative vertebrates.

A final question is why the banded mongooses exhibit a one-to-one escort system of pup care, while other social mongooses do not? Answering this question is difficult because to our knowledge the escort system is unique among cooperative vertebrates: in no other system do nonbreeders develop exclusive dyadic-caring relationships with particular pups. The most plausible explanation is that differences between mongoose species in pup foraging strategies reflect differing profitability for pups of "sampling" from a single versus multiple helpers. Where resources are patchy and scarce (as in meerkats, and possibly dwarf mongooses), pups may need to beg from multiple helpers to obtain a minimum threshold amount of resources. In the banded mongooses in Uganda, insect food is much more abundant, and pups apparently do best to aggressively monopolizing access to good helpers. Banded mongooses are widely distributed in sub-Saharan Africa and are sympatric with dwarf mongooses in some locations (e.g. Serengeti; Waser et al., 1995; Sengwa, Zimbabwe; M Cant, personal observations). Information on the fidelity of helper–pup relationships in the banded mongooses and dwarf mongooses living in these habitats would help to understand the evolution of escorting, and further explore the causal consequences of this one-to-one relationship for the pup development, health, and learning.

## 6. CONCLUSIONS

### 6.1. Social Evolution: Theory Meets Reality

Social evolution theory has developed rapidly in the last 20 years, particularly in the study of reproductive skew and selection in viscous populations. As is often the case in behavioral ecology, however, the theoretical advances have far outpaced empirical testing of the models. The result is a range of models each based on different assumptions which make distinct or overlapping predictions. For example, in the study of reproductive skew, over 15 different models were published in the 5 years between 1998 and 2003 (Gardner & Foster, 2008); in the study of cooperation in viscous populations, over 20 models have appeared since Taylor's (1992) first analysis using the infinite island framework (Lehmann & Rousset, 2010). The main need now is for empirical studies to weed out mechanisms or assumptions that do not hold in nature, and to suggest new mechanisms or assumptions to form the basis of theoretical work that is solidly grounded on observations and experiment.

For reproductive skew theory, our results highlight how the effectiveness of threats of departure, eviction, or attack (or lack thereof) determines the distribution of reproduction among group members, and the frequency with which aggressive acts are observed. Threats of dispersal are irrelevant since the benefits of group membership are so high; threats of eviction and infanticide are typically ineffective most likely because of informational constraints, which mean that transgressors can often escape punishment. The inability of dominants to deter subordinate reproduction using threats contributes to the dynamic nature of these social groups, with large fluctuations in group size, mass evictions, group extinction, and group founding. To understand population dynamics of banded mongooses, and cooperative mammals more generally, requires knowledge of the behavioral strategies employed in reproductive conflict, and the physical and informational constraints on those strategies. We believe that in many other cooperative vertebrates, there will be strong links between reproductive conflict, gene-flow, and population dynamics. Hopefully, a second wave of research on skew and reproductive conflict is forthcoming, grounded and informed by long-term studies of cooperative breeders.

For demographic models of social evolution, researches on the banded mongoose and other cooperatively breeding vertebrates provide opportunities to test existing models, but also suggest areas where new theory is required. In particular, more work is needed to understand the causes and consequences of forced eviction from viscous groups—when should subordinates leave versus wait to be pushed? In many cases dispersers could gain from leaving together as a group, but require third party intervention to solve the coordination problem of who leaves first. From the perspective of evictors, which individuals are targeted for dispersal may depend on the mortality rate or success rate of dispersers. Where dispersal is sufficiently easy, dominants may be selected to target closer relatives for eviction, since this would ensure that budding coalitions consist of genetically similar individuals. On the other hand, if dispersal is sufficiently costly, dominants may do best to evict more distant relatives and leave closer relatives to inherit breeding status in their natal group later in life. There may also be a component of positive feedback in the size of evicted groups: once group dispersal is common, evictors may need to expel larger numbers of their offspring to ensure the success of dispersing coalitions. Formal kin selection and game theory models of budding by eviction could help to evaluate these verbal arguments.

Theoretical research on evolution in structured populations suggests that behavioral ecologists working on cooperative breeders may need to radically rethink their concept of fitness and how to measure it in natural populations. In structured populations, fitness is a measure of the relative success of with which group members can export copies of their alleles to other groups, by producing dispersers which usurp existing groups or found new ones. This type of fitness concept is sometimes referred to as "metapopulation fitness" because each group (or deme) in the population can be thought of as a miniature population embedded within the metapopulation. For example, Metz and Gyllenberg (2001) suggest defining fitness in structured populations as "the average number of newborn dispersing individuals resulting from the local colony founded by a newborn disperser". In a system such as banded mongooses, fitness might be similarly defined as the average number of emigrants produced by a successful group founder or usurper. These definitions are very different from the usual measures of fitness employed in field studies, namely the average or lifetime number of surviving offspring. In long-lived cooperative breeders, selection on fertility and mortality, and on social behavior across the lifespan, depends on the age and sex of dispersers, and the way in which the life history of one generation overlaps or tessellates with the life history of other generations in the same social group (Cant & Johnstone, 2008; Johnstone & Cant, 2010). Future theoretical works to further incorporate demography into models of social evolution, and measures of metapopulation fitness in wild cooperative vertebrates, offer the best hope of developing a unified "social life history theory" applicable to animal societies from insects to humans.

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