

*Review*

# Structure and function in mammalian societies

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Traditional interpretations of the evolution of animal societies have suggested that their structure is a consequence of attempts by individuals to maximize their inclusive fitness within constraints imposed by their social and physical environments. In contrast, some recent re-interpretations have argued that many aspects of social organization should be interpreted as group-level adaptations maintained by selection operating between groups or populations. Here, I review our current understanding of the evolution of mammalian societies, focusing, in particular, on the evolution of reproductive strategies in societies where one dominant female monopolizes reproduction in each group and her offspring are reared by other group members. Recent studies of the life histories of females in these species show that dispersing females often have little chance of establishing new breeding groups and so are likely to maximize their inclusive fitness by helping related dominants to rear their offspring. As in eusocial insects, increasing group size can lead to a progressive divergence in the selection pressures operating on breeders and helpers and to increasing specialization in their behaviour and life histories. As yet, there is little need to invoke group-level adaptations in order to account for the behaviour of individuals or the structure of mammalian groups.

**Keywords:** societies; evolution; mammals; cooperation; reproductive strategies; life-histories

## 1. INTRODUCTION

Early attempts to explain the evolution of animal and human societies argued that their structure has important functions for the lives of individuals (Kropotkin 1908; Richards 1939; Radcliffe Brown 1952; Wynne-Edwards 1962; Gartlan 1968). In contrast, most modern interpretations of the evolution of animal societies have focused on the evolution of reproductive strategies in individuals and have interpreted variation in the structure of societies (including contrasts in the size and structure of groups, in patterns of interaction between group members and in the form of mating systems) as by-products of the evolution of individual strategies (Crook *et al.* 1976; Clutton-Brock 1989*c*; Krebs & Davies 1993; Kitchen & Packer 1999). Over the last 50 years, this approach has led to dramatic developments in our understanding of the evolution of parental investment (Trivers 1972), fighting strategies (Parker 1974), mate choice (Andersson 1994), nepotism (Hamilton 1964; Emlen 1991) and cooperation (Dugatkin 1997; Nowak 2006), which, in turn, have provided a framework for explaining species differences in the size, age, sex and kinship structure of groups, in the contribution of females and males to parental care and in the structuring of interactions between individuals

(Jarman 1974; Bradbury & Vehrencamp 1976, 1977; Clutton-Brock & Harvey 1977; Wrangham 1980; Rood 1986; Clutton-Brock 1989*c*).

In this paper, I briefly review our understanding of the evolution of mammalian societies. As polygynous breeding systems are common among mammals while cooperative societies are rare, I initially review our understanding of polygynous societies, which are often characterized by intense competition between males. Subsequently, I focus on societies where young are raised primarily by non-breeding group members and reproductive competition between females is intense. Though these societies occur in a small proportion of social mammals, the evolution of non-breeding helpers provides an important challenge to our understanding of social evolution and mammals include the most specialized cooperative breeding systems found among vertebrates (Alexander *et al.* 1991; Sherman *et al.* 1991; Clutton-Brock 2006). A review of the evolution of cooperative societies is timely since recent re-evaluations of the role of group selection have suggested that many cooperative activities and aspects of group structure in social mammals represent group-level adaptations rather than by-products of the adaptive strategies of individuals (Wilson & Wilson 2007). In the final discussion, I briefly compare the cooperative breeding systems of mammals with those of birds and social insects and reassess arguments that cooperative societies should be interpreted as group-level adaptations.

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## 2. THE EVOLUTION OF MAMMALIAN POLYGYNY

In many mammals, females either form unstable groups or herds consisting primarily of unrelated individuals or live in stable groups consisting primarily of matrilineal relatives (Clutton-Brock 1989c). In addition, in a small number of species, females normally disperse from their natal group at adolescence and (as in many group-living birds) stable groups consist of several unrelated females defended by one or more males (Clutton-Brock 1989b). Where females live in stable groups with matrilineal relatives, group members often cooperate to defend feeding or breeding territories, though non-territorial groups of related females are also common, especially in large, wide-ranging species. The benefits of aggregation to females vary between species, but include improved detection of and defence against predators, benefits associated with social foraging or hunting and advantages in competition with neighbouring groups (Bertram 1978; Clutton-Brock & Harvey 1978; Wrangham 1980; Van Schaik 1983). In addition, in a small number of species where females form stable groups with matrilineal relatives, they cooperate to rear young (see below).

The fundamental structure of female groups and the distribution of cooperative behaviour in mammals consequently show many parallels with the structure of groups in social insects (Boomsma 2007, 2009; Helanterä & Bargum 2007). In contrast, in most birds, breeding females form breeding pairs with a single male, often defending nest sites or feeding territories against other females (Lack 1968). While colonies are common in species where food supplies cannot be economically defended, they are typically open aggregations of unstable membership, consisting of multiple socially monogamous pairs (Lack 1968). In bird species where females form stable groups and share access to a group range or territory, one female usually monopolizes reproduction, her female offspring typically disperse at adolescence (so that female group members are seldom close relatives), and cooperation between females is seldom highly developed (Greenwood 1980; Koenig & Haydock 2004). The likely reason why female mammals more commonly form stable groups that include multiple breeding females than birds is that many mammals are able to feed largely or exclusively on vegetable matter whose relative abundance frees females from dependence on male assistance in rearing young and permits local population densities and biomass to reach higher levels than in birds (figure 1). As might be expected, monogamous breeding systems and dispersal of adolescent females are both relatively common in carnivorous mammals (Kleiman 1977; Gittleman 1989) while their population density is relatively low (McNab 1980).

The frequent aggregation of female mammals in stable groups combined with their capacity to rear young independently allows individual males to guard multiple mating partners, leading to the evolution of pre-copulatory mate guarding and polygynous mating systems. Variation in the size, stability and ranging patterns of female groups affect the defensibility of females by males and the degree of polygyny and consequently affect variance in male reproductive success, the

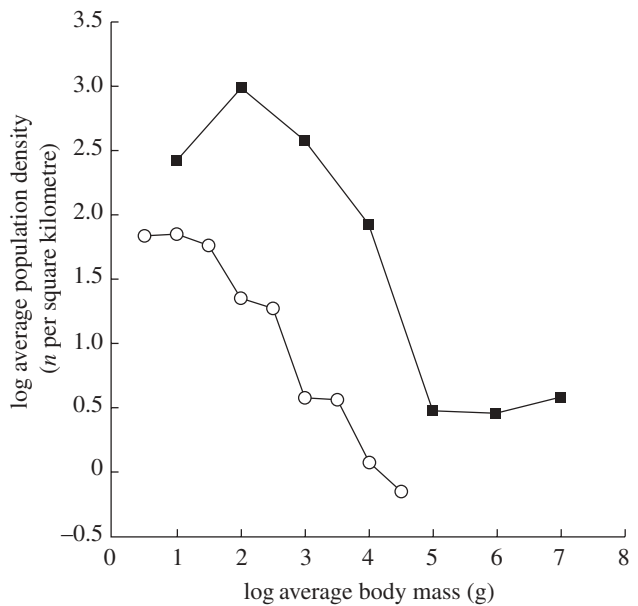


Figure 1. Variation in population density of North American birds (open circles) and mammals (filled squares) of different body mass (adapted from Silva *et al.* 1997).

strength of selection pressures favouring characteristics influencing competitive success in males (such as body size or weapon development) and the evolution of sex differences in behaviour, physiology and anatomy (Bradbury & Vehrencamp 1977; Wade & Arnold 1980; Clutton-Brock 1983, 1989c; Clutton-Brock *et al.* 1993). In many mammals, intense competition combined with the limited ability of females to evade persistent males has favoured the evolution of coercive strategies and male infanticide (Hrdy 1977; Smuts & Smuts 1993; Clutton-Brock & Parker 1995; Ebensperger 1998a; Van Schaik 2000) with important consequences both for female mating preferences (Ebensperger 1998b; Clutton-Brock & McAuliffe 2009) and for associated selection pressures on the reproductive anatomy of males (Harcourt *et al.* 1981).

Intense competition between males in polygynous mammals and associated adaptations, such as increased male body mass, generate energetic costs and increase the risk of injury: in highly polygynous species, adult males are commonly more susceptible to starvation than females, have higher annual rates of mortality than females, age more quickly and die at younger ages (Trivers 1972; Clutton-Brock *et al.* 1982b, 1985; Clutton-Brock & Isvaran 2007; Donald 2007). One important consequence of the relatively short breeding lifespans of males in polygynous species is that, in many societies, relatively few females reach breeding age in groups where their father still monopolizes access to receptive females, so that females can remain and breed in their natal group without risking inbreeding, allowing the development of kin-based female groups (Clutton-Brock 1989a). In contrast, in vertebrates where males have breeding lifespans that are typically longer than the age of females at first breeding (including a few social mammals and many group-living birds), females frequently reach maturity while their father is still reproductively active and typically disperse at adolescence (Clutton-Brock 1989c), so that

adult female group members are usually unrelated to each other (Greenwood 1980; Clarke *et al.* 1997).

### 3. REPRODUCTIVE COMPETITION BETWEEN FEMALES

Since Darwin's time, the intensity of male competition and the evolution of striking secondary sexual characters in males initially focused the attention of biologists on the evolution of male strategies and traits (Darwin 1871/1958; Andersson 1994). Only more recently has it come to be appreciated that life in stable social groups also generates intense reproductive competition and large individual differences in female breeding success which can have far-reaching consequences for selection pressures operating on both sexes, for the evolution of life histories and reproductive strategies and for the structure of societies (Hauber & Lacey 2005; Clutton-Brock *et al.* 2006; Clutton-Brock 2007, 2009). As local populations approach the carrying capacity, female group members compete for resources, and frequent interactions between the same individuals commonly generate dominance hierarchies where the status of individuals is associated with consistent differences in resource access, fecundity and rearing success (Clutton-Brock *et al.* 1982a, 1984; Walters & Seyfarth 1986; Holekamp & Swale 2000). However, females do not show obvious hierarchies in all social species: for example, there is little evidence of consistent differences in social status among African lions (*Panthera leo*) and individual differences in reproductive success are small (Packer *et al.* 2001). Where female groups are sufficiently large that they include females belonging to more than one matriline, female relatives commonly support each other and are intolerant of offspring born to subordinate matriline, who often show relatively low survival (Silk *et al.* 1981; Holekamp *et al.* 1996). In some macaques, dominant females even focus their aggression on female juveniles born to subordinate mothers who, unlike males, will remain in the group and so represent potential competitors for their own offspring (Dittus 1979; Silk *et al.* 1981).

In a substantial number of mammalian societies, females direct regular aggression against other breeding females and commonly attempt to interfere directly with their breeding attempts, killing their young when opportunity arises (Ebensperger 1998a; Digby 2000) and (Ebensperger 1998a; Digby 2000; Clutton-Brock 2009). As groups typically consist of matrilineal relatives, competitors are usually kin but proximity of kinship appears to have little effect on the probability of infanticidal behaviour, which is typically directed at likely competitors, however closely they are related (Hoogland 1995). In extreme cases, competition between females can lead to situations where only one female per group breeds regularly and, as in most eusocial insects, many females never breed successfully at any stage of their lifespan (Creel & Waser 1997; Faulkes & Abbott 1997; Creel & Creel 2001; Hauber & Lacey 2005; Clutton-Brock *et al.* 2006).

### 4. REPRODUCTIVE SUPPRESSION

While occasional cooperation occurs in many social mammals, cooperative breeding systems (where young

born to one or more breeding females in each group are reared by non-breeding helpers) are rare and are most highly developed in four groups: the marmosets and tamarins (Callitrichidae) (Goldizen 1987a,b; Digby *et al.* 2007); the dogs (Canidae) (Moehlman 1986; Creel & Creel 2001); diurnal mongooses (Herpestidae) (Rood 1986; Creel & Waser 1997; Clutton-Brock 2006) and African mole-rats (Bathyergidae) (Bennett & Faulkes 2000; Faulkes & Bennett 2007). Cooperative systems in these four groups range from species living in monogamous pairs, occasionally assisted by one or two young from the previous breeding season where parents are responsible for a high proportion of parental care, as in silver-backed jackals (*Canis mesomelas*; Moehlman 1986) to naked mole-rats (*Heterocephalus glaber*), where groups can consist of more than 100 individuals. These groups include a single breeding male and a single breeding female, who are unable to rear young successfully without helpers (Sherman *et al.* 1991), and breeding females share a number of traits with queens in social insects, including enhanced body size, dominance over all other colony members and unusually long lifespans (Braude 1991; Brett 1991; Sherman *et al.* 1991; Sherman & Jarvis 2002; Faulkes & Bennett 2007).

The kinship structure of breeding groups varies widely. In some species, breeding females and helpers of both sexes have usually been born in the group while breeding males are immigrants (meerkats, *Suricata suricatta*, Damaraland mole-rats, *Cryptomys damarensis*); in others, breeding females are typically immigrants while breeding males have often been born in the group (African wild dogs, *Lycaon pictus*, some marmosets); in some, breeders of either sex may either be immigrants or nats (marmosets and tamarins, banded mongooses, *Mungos mungo*) and in a few, breeders of both sexes are usually nats (naked mole-rats). As in birds (Bennett & Owens 2002; Blumstein & Møller 2008), there are no simple associations in mammals between cooperative breeding and diet or habitat; in mammals, cooperative breeders include herbivores (the mole-rats), frugivores and gumivores (the callitrichid primates), insectivores (the mongooses) and carnivores (the canids) (Clutton-Brock 2006). The likely benefits of sociality and cooperation vary between groups, ranging from the maintenance of extensive tunnel systems in mole-rats, improved hunting success in the larger canids, transport of dependent offspring in the callitrichids and cooperative detection of predators and defence in the diurnal mongooses (Clutton-Brock 2006).

In many cooperative mammals, dominant females routinely evict subordinate females, though the age at which dominants evict subordinates varies with important consequences for the age structure and size of groups. In the callitrichid primates and the smaller canids, resident breeding females are usually intolerant of other adult females, who are either evicted or disperse voluntarily. As a result, groups commonly contain a single fully adult female and a variable number of males, which may include a mixture of nats and immigrants (Moehlman & Hofer 1997; Creel & Creel 2001; Goldizen 2003; Digby *et al.* 2007). In meerkats, which live in larger groups,

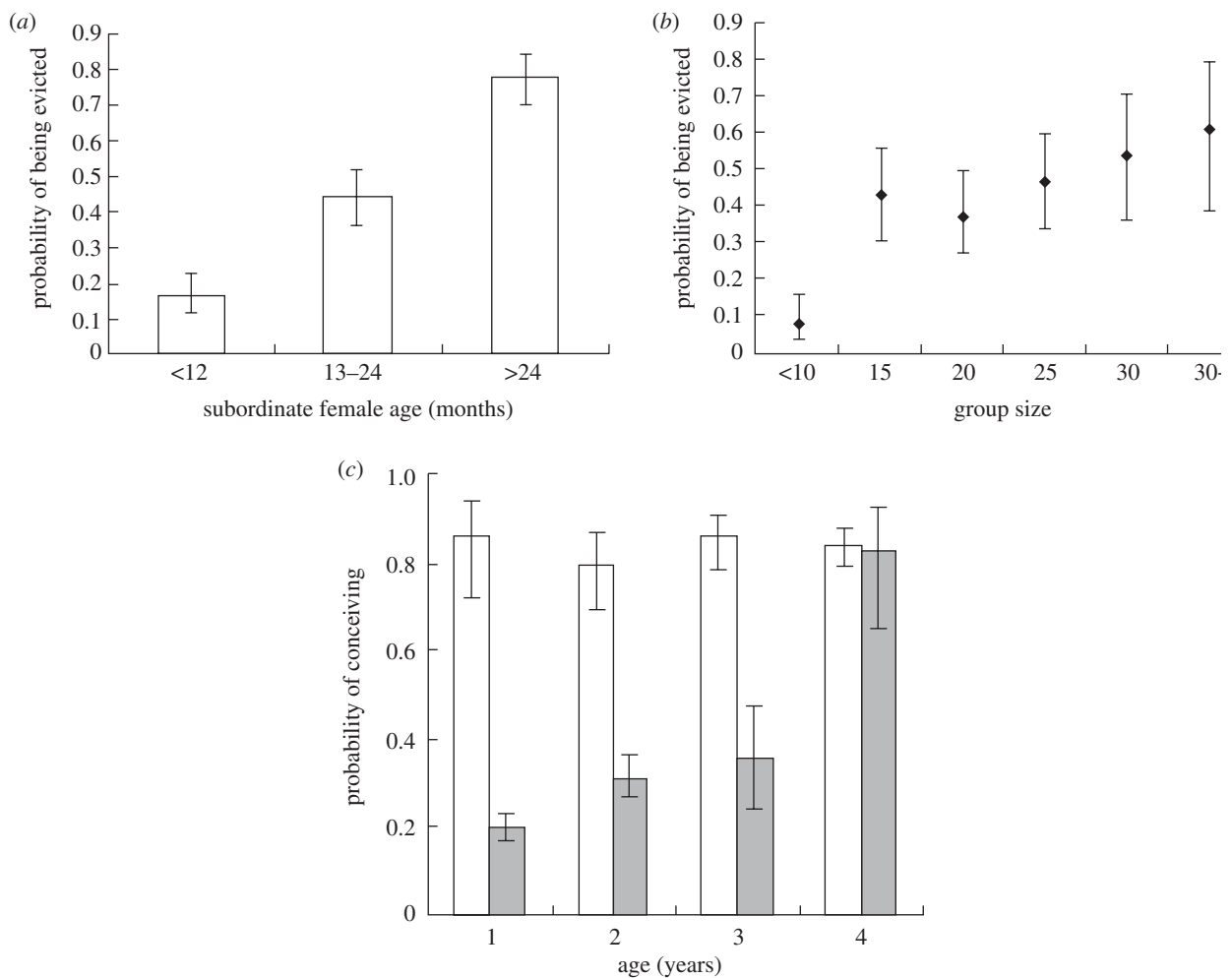


Figure 2. Eviction of subordinate females in meerkats: (a) the probability that subordinate females will be evicted by dominant females in their first, second and third year of life; (b) the probability that subordinate females will be evicted from groups of different size; (c) the probability that subordinates (shaded bars) and dominants (open bars) conceive during a three-month period at different ages (adapted from Clutton-Brock *et al.* 2008).

dominant females tolerate adult subordinate females for 1 or 2 years after they are sexually mature, directing increasingly frequent aggression at older or heavier subordinates and eventually evicting all females before they are 5 years old (Clutton-Brock *et al.* 1998b, 2001a; Young & Clutton-Brock 2006; Young *et al.* 2006; Clutton-Brock *et al.* 2008) (figure 2a). Though groups of evictees are sometimes able to establish new breeding groups, the new dominant soon evicts them again, so that virtually all females are either dominant or dead by the time they are 4 years old, while males disperse to breed in other groups at around the same age. In naked mole-rats, subordinate females rarely disperse and may remain in their natal group throughout their lives, so that colonies contain subordinates of a wide range of ages (Brett 1991; Sherman & Jarvis 2002). When dominant females die and a new dominant female has established herself, she kills or evicts her competitors within the next year (Reeve & Sherman 1991) (P. Sherman 2006, personal communication). In naked mole-rats, males, too, usually remain in the colony, though a proportion adopt a divergent growth trajectory and disperse when conditions are favourable (O'Riain *et al.* 1996). How commonly dominant breeding males in natural groups are immigrants versus natals is not yet known.

Dominant females also suppress the fecundity of subordinate females, and frequently kill any offspring they produce, though the extent to which the reproductive function of subordinates is suppressed varies widely. In many societies, subordinate females show lower levels of luteinizing hormone (LH) or oestrogen than dominant females either throughout the breeding season or over the period of oestrous (Abbott 1984; French 1997; O'Riain *et al.* 2000a; Creel & Creel 2001). In some species (including meerkats), differences in LH levels disappear when subordinates are challenged with gonadotropin-releasing hormone (GnRH), indicating that suppression can be quickly reversed. In others (including marmosets and naked mole-rats), differences in LH levels between dominants and subordinates persist, indicating that reproductive function is more deeply suppressed (Abbott 1993; Faulkes & Abbott 1997; French 1997). However, even here, the removal of dominant females or the provision of access to unrelated males leads to relatively rapid increases in levels of sex hormones and reproductive competition in subordinates (Faulkes *et al.* 1997; Cooney & Bennett 2000). In naked mole-rats (but not, as yet, in other species), dominant females also suppress the development of subordinate males (Faulkes & Abbott 1997).



(M. J. O’Riain 2006, personal communication), possibly because subordinate females will mate with close relatives so that natal males are prospective breeding partners.

Because breeding females are frequently the mothers or sisters of subordinate females, suppressing the development of subordinates, killing their pups or evicting them from the group are likely to have substantial costs to the inclusive fitness of dominants. So why do dominants suppress subordinate reproduction in most cooperative breeders? The likely answer is that female group members have the capacity to produce more young than the group is able to raise and that simultaneous litters dilute the investment of helpers and reduce the growth and survival of offspring born to the dominant females (Hodge 2009). Experimental increases in the size of meerkat litters reduce the food intake and growth of pups, which are closely related to their survival (Clutton-Brock *et al.* 2001b). In addition, where helpers raise litters born to dominants at the same time as litters born to subordinate mothers, the growth of the dominant female’s pups is reduced if older pups are present (Hodge 2009). As would be expected, the extent to which dominants tolerate subordinates appears to vary in relation to the risk of reproductive competition. In meerkats, dominant females are more likely to evict subordinates and to kill their pups if they themselves are pregnant than if they are not (Clutton-Brock *et al.* 1998b). The age at which they evict subordinates coincides with increases in the probability that subordinates will attempt to breed if they remain in the group (figure 2b) (Clutton-Brock *et al.* 2008) and they are also more likely to evict individuals if they have attempted to breed or which are relatively distant relatives (Young *et al.* 2006; Clutton-Brock *et al.* 2008).

Dominant females do not attempt to prevent subordinates from breeding in all cooperative species and, in some, including African lions and banded mongooses, multiple females breed regularly (Lewis & Pusey 1997; Russell 2004; Clutton-Brock 2006). Evidence of the benefits of suppressing subordinate reproduction to dominants (Hodge 2009) prompts the related question why breeding females do not always suppress subordinates. One possible explanation is that subordinate breeding does not reduce the breeding success of dominants in all cooperative breeders. For example, in banded mongooses, where multiple females commonly breed in synchrony, the pups of dominant females show higher survival rates if one or more subordinate females breed at the same time as the dominant than if they do not, though why this is the case is not yet fully clear (Hodge 2003, 2009). An alternative or additional possibility is that, in some societies, the costs of suppression to dominant females may be very high. For example, the possession of lethal weaponry by lionesses may effectively preclude both established dominance relations and any form of reproductive suppression (see Packer *et al.* 2001).

## 5. SUBORDINATE STRATEGIES

By their persistent attempts to prevent subordinate females from breeding, dominant females restrict the

reproductive options of subordinates in high skew societies to three main alternatives: disperse in an attempt to form a new breeding group elsewhere and establish themselves as the dominant female in it; challenge the existing dominant for her position; or remain in the natal group, with the possibility either of breeding as a subordinate when the dominant’s ability to control subordinate reproduction is reduced or of inheriting the breeding position on her death. In many high-skew societies where females live in stable groups, none of these three options offers a substantial chance of successful reproduction to the majority of subordinates. In species that live in territorial, matrilineal groups, such as meerkats or mole-rats, female immigration is usually resisted by all group members whether local density is saturated or not and successful immigration by females into established groups is very rare. Without other individuals to assist them, solitary females seldom survive for long and, even if several dispersing females manage to establish a new group, only one will acquire the dominant position and the others will rapidly be evicted to face an uncertain future again (Clutton-Brock *et al.* 1998b, 2006; Young & Clutton-Brock 2006). In addition, the chances that a newly established dominant female will breed successfully are low, because group size and helper number are likely to be low (Clutton-Brock 1998; Clutton-Brock *et al.* 2001a; Courchamp *et al.* 2003). As a result, it is unsurprising that, in many cooperative mammals, including meerkats and naked mole-rats, subordinate females only leave their natal group if they are evicted by force and make extensive efforts to induce the dominant female to allow them to remain (Clutton-Brock *et al.* 1998b; Kutsukake & Clutton-Brock 2006).

Challenging the established dominant is also rarely successful. In some species, including naked mole-rats, and, to a lesser extent, in meerkats, individuals that acquire dominant status increase in size and body mass and show increased levels of testosterone so that subordinate females are unlikely to win contests with established dominants (Faulkes & Abbott 1997; O’Riain *et al.* 2000b; Russell *et al.* 2004) (figure 3a). In addition, dominant females may evict subordinates before they reach full adult size (figure 2). Moreover, replacing an established breeder may reduce the challenger’s inclusive fitness if the breeding female is a close relative for, in many cooperative breeders, the annual breeding success of new breeders is low (Woolfenden & Fitzpatrick 1984; Waser *et al.* 1995; Creel & Creel 2001; Sherman & Jarvis 2002; Hodge *et al.* 2008). As a result, it may seldom benefit mature daughters to attempt to replace dominant mothers where their father is still the resident breeding male, so that subsequent offspring produced by their mother will be full sibs (see Bourke 2007).

As in eusocial insects (see Keller & Nonacs 1993; Beekman & Ratnieks 2003; Beekman *et al.* 2003; Hart & Ratnieks 2005; Keller 2009; Ratnieks & Helanterä 2009), there has been a longstanding debate as to whether reproductive suppression in subordinate mammals is best interpreted as a consequence of constraints imposed by dominants or is better interpreted as the outcome of reproductive

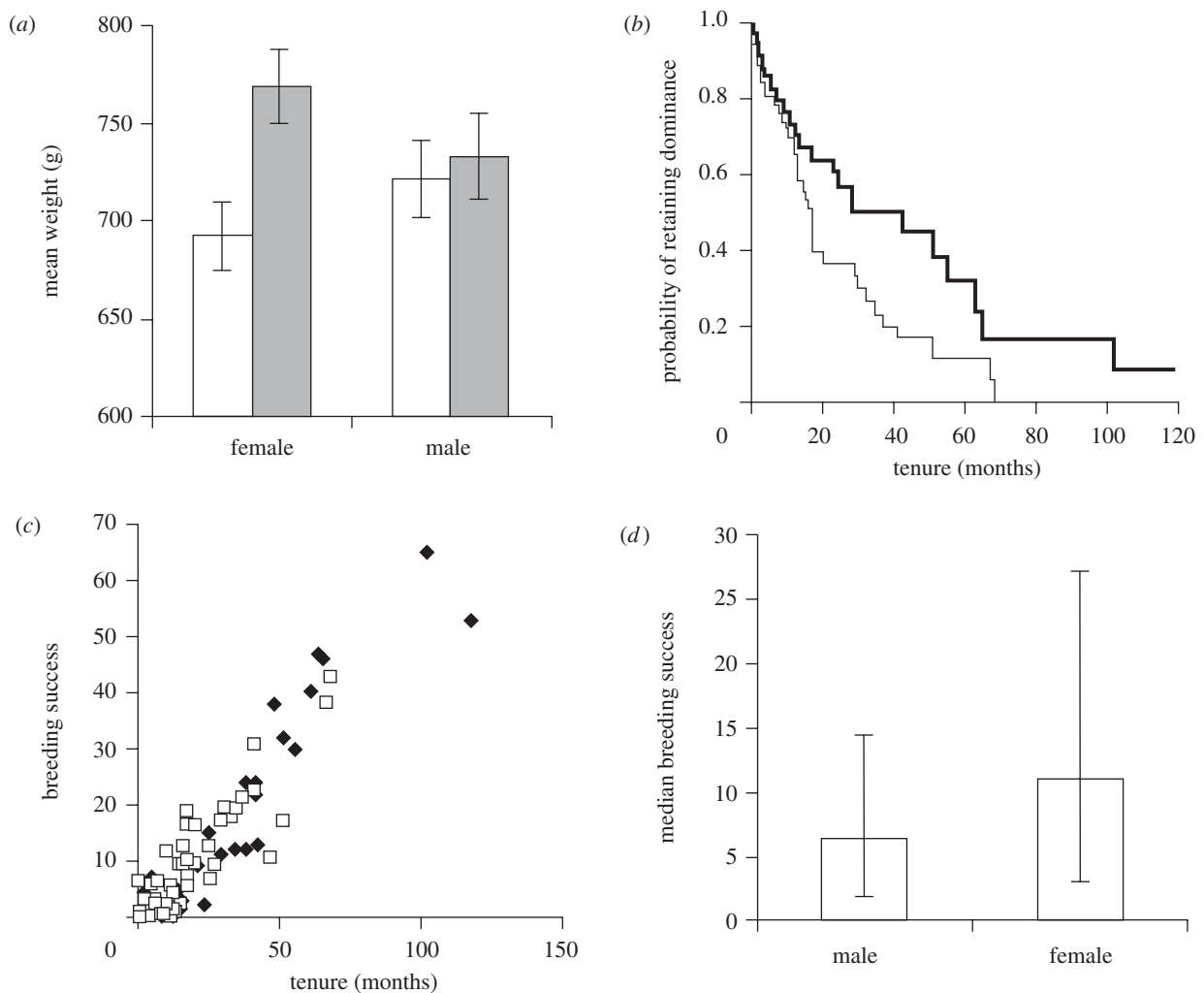


Figure 3. (a) Mean mass of females and males that acquired dominant status three months before becoming dominant and six months after becoming dominant (unfilled bar, subordinate; filled bar, dominant); (b) probability (Kaplan–Meier estimates) of dominant female (thick line) and male (thin line) meerkats in a naturally regulated population retaining their status for different periods of time; (c) cumulative reproductive success of female (filled diamonds) and male (open squares) meerkats with increasing tenure and (d) mean breeding success of females and males that acquire dominant status in their group (adapted from Clutton-Brock *et al.* 2006).

restraint by subordinates (Creel & Creel 2001; Young *et al.* 2006). Aspects of their phenotype (including their condition, foraging ability and reproductive experience) as well as their social and ecological circumstances and the likely response of the dominant female to any breeding attempts will affect the pay-offs of breeding attempts to subordinates (Ratnieks & Wenseleers 2008; Ratnieks & Helanterä 2009). In theory, examples of ‘pure’ restraint could evolve in cooperative societies if the presence and behaviour of dominants had no effect on the pay-offs of breeding attempts to subordinates but, as in social insects, the presence and behaviour of dominant females usually appears to play an important role in determining the pay-offs of breeding attempts (see Ratnieks & Helanterä 2009). As the characteristics of subordinates will also affect the outcome of breeding attempts, and interactions are likely to be common, attempts to distinguish between adaptive constraint and reproductive restraint are a rather theoretical exercise.

Where the chances that individual subordinates will acquire the breeding position are low and subordinates

are unlikely to breed successfully, the relative benefits of increasing the indirect component of their inclusive fitness by assisting in rearing young born to related dominants (who commonly are either their mother or their sister) are likely to be relatively large (West-Eberhard 1975, 1981; Sherman *et al.* 1995; Shellman-Reeve 1997; Bourke 1999; Ratnieks & Helanterä 2009). In meerkats and wild dogs, as well as in several cooperative birds, assistance has substantial effects on the growth of the dominant female’s offspring, the frequency with which she breeds and the survival of her offspring (Clutton-Brock *et al.* 2001b; Creel & Creel 2001; Russell *et al.* 2003a). Moreover, the contributions of individual helpers to cooperative rearing are usually conditional on their weight, age and reproductive condition, so that the costs of helping to their own growth and fitness are likely to be low (Wright *et al.* 2000; Clutton-Brock *et al.* 2002; Russell *et al.* 2003b). However, opportunistic attempts to breed as a subordinate when the dominant female’s control is relaxed may often provide subordinates with the best chance of direct reproduction and are

common in some species (Clutton-Brock *et al.* 2001a; Creel & Creel 2001; Clutton-Brock *et al.* 2008). Where breeding increases the risk that the subordinate will attract aggression from the dominant female and be evicted (see Young *et al.* 2006), subordinates would be expected either to attempt to disguise their reproductive status or to placate dominants, and there is some evidence of strategies of this kind. In meerkats, for example, older and heavier female subordinates that are likely to be evicted by dominant females commonly attempt to groom dominants and readily submit to minor threats (Kutsukake & Clutton-Brock 2006).

Subordinates might also be expected to adjust their relative investment in cooperative behaviour in relation to their chances of breeding successfully. Recent studies of mole-rats provide convincing evidence of strategies of this kind. In Damaraland mole-rats, subordinates can be divided into frequent and infrequent helpers (Scantlebury *et al.* 2006). Infrequent workers increase their daily energy expenditure after rainfall and may be more likely to disperse, while frequent workers do not. Similarly, in naked mole-rats, some males show increased growth and fat deposits, reduced levels of cooperative behaviour and an increased probability of dispersing (O'Riain *et al.* 1996).

## 6. ADAPTATIONS OF BREEDING FEMALES IN HIGH-SKEW SOCIETIES

In the more specialized cooperative vertebrates where reproductive skew is pronounced, dominant females often show unusual adaptations that resemble the characteristics of queens in eusocial insects (Alexander *et al.* 1991). Both in meerkats and naked mole-rats, levels of circulating testosterone rise in females that acquire the breeding position and, although they are already fully adult, dominant females increase in size and body mass (Faulkes & Abbott 1997; O'Riain *et al.* 2000b; Russell *et al.* 2004; Clutton-Brock *et al.* 2006) (see figure 3a). Studies of meerkats show that increases in the number of helpers reduce the costs of breeding to the dominant female and the interval between successive litters, leading to increases in her rate of reproduction (Clutton-Brock *et al.* 1998a; Russell *et al.* 2003a) and, both in meerkats and in social mole-rats, dominant females show unusually high levels of fecundity, conceiving again shortly after giving birth and producing multiple litters per year (Jarvis 1991a; Clutton-Brock *et al.* 2001a; Russell *et al.* 2003a).

Cooperative breeding is also associated with relatively long lifespans in breeding females (Arnold & Owens 1998; Carey 2001; Sherman & Jarvis 2002). In meerkats, where breeding females forage independently and so are exposed to a regular extrinsic risk of mortality, dominant females can continue to breed for 8–10 years (figure 3b) and in several of the social mole-rats, breeding females can also live for 10 years or more (Dammann & Burda 2006) (N. Bennett 2009, personal communication). In naked mole-rats, breeding females have even longer lifespans and can breed for more than 20 years (Sherman & Jarvis 2002). Though no studies of wild populations

have yet documented ageing rates and studies of captive colonies have produced variable results (Sherman & Jarvis 2002; Ross-Gillespie *et al.* 2007) (M. J. O'Riain 2006, personal communication), it seems likely that the social mole-rats, like some eusocial insects (Carey 2001), have evolved mechanisms that defer senescence in breeding females. Comparisons between naked mole-rats and mice show that protein structural stability, oxidation and degradation show relatively little change with increasing age in naked mole-rats (Perez *et al.* 2009). In addition, broader comparisons between small mammals with relatively long lifespans and species with relatively short ones show that long-lived species maintain tightly regulated basal levels of vitamin D, insulin, glucocorticoid and thyroid endocrine systems (Buffenstein & Pinto 2009).

As a result of high levels of reproductive skew, rapid rates of reproduction and relatively long lifespans, individual differences in breeding success among females are often unusually large in cooperative breeders (Hauber & Lacey 2005; Clutton-Brock *et al.* 2006). For example, in meerkats, successful breeding females can rear up to a hundred surviving offspring during their lives (figure 3c) while, in naked mole-rats, this may rise to over 1000 (Sherman & Jarvis 2002). Because the majority of females fail to breed altogether (Clutton-Brock *et al.* 2006), selection pressures on females favouring traits associated with the acquisition and maintenance of the dominant position, like relative weight can be extremely strong. In meerkats, heavier females are more likely to acquire and maintain dominant status (figure 4a,b) and their daughters are also more likely to do so in their turn (figure 4c). The intensity of selection on traits associated with competitive success in females probably explains why they show more pronounced changes in hormonal status and growth than males after they acquire alpha status (Faulkes & Abbott 1997; Russell *et al.* 2004; Clutton-Brock *et al.* 2006).

## 7. ADAPTATIONS OF MALES IN HIGH-SKEW SOCIETIES

High reproductive skew in females also has important consequences for males. The restriction of effective female reproduction to one relatively long-lived breeding female per group typically limits the opportunity for polygyny in males and favours close mate guarding and monogamous breeding (Clutton-Brock 2006). In many of the specialized cooperative breeders, a single male guards reproductive access to the breeding female and extra-pair paternity appears to be rare. For example, in meerkat groups, one dominant male monopolizes breeding access to the dominant female and sires over 90 per cent of her young (Griffin *et al.* 2003; Spong *et al.* 2008). In naked mole-rats too, a single male monopolizes access to the breeding female (Jarvis 1991a; Bennett & Faulkes 2000) while, in African wild dogs and callitrichids, groups commonly include several breeding males and multiple males may mate but subordinates apparently sire few offspring (Girman *et al.* 1997; Creel & Creel 2001; Goldizen 2003; Heyman 2003). In this respect,

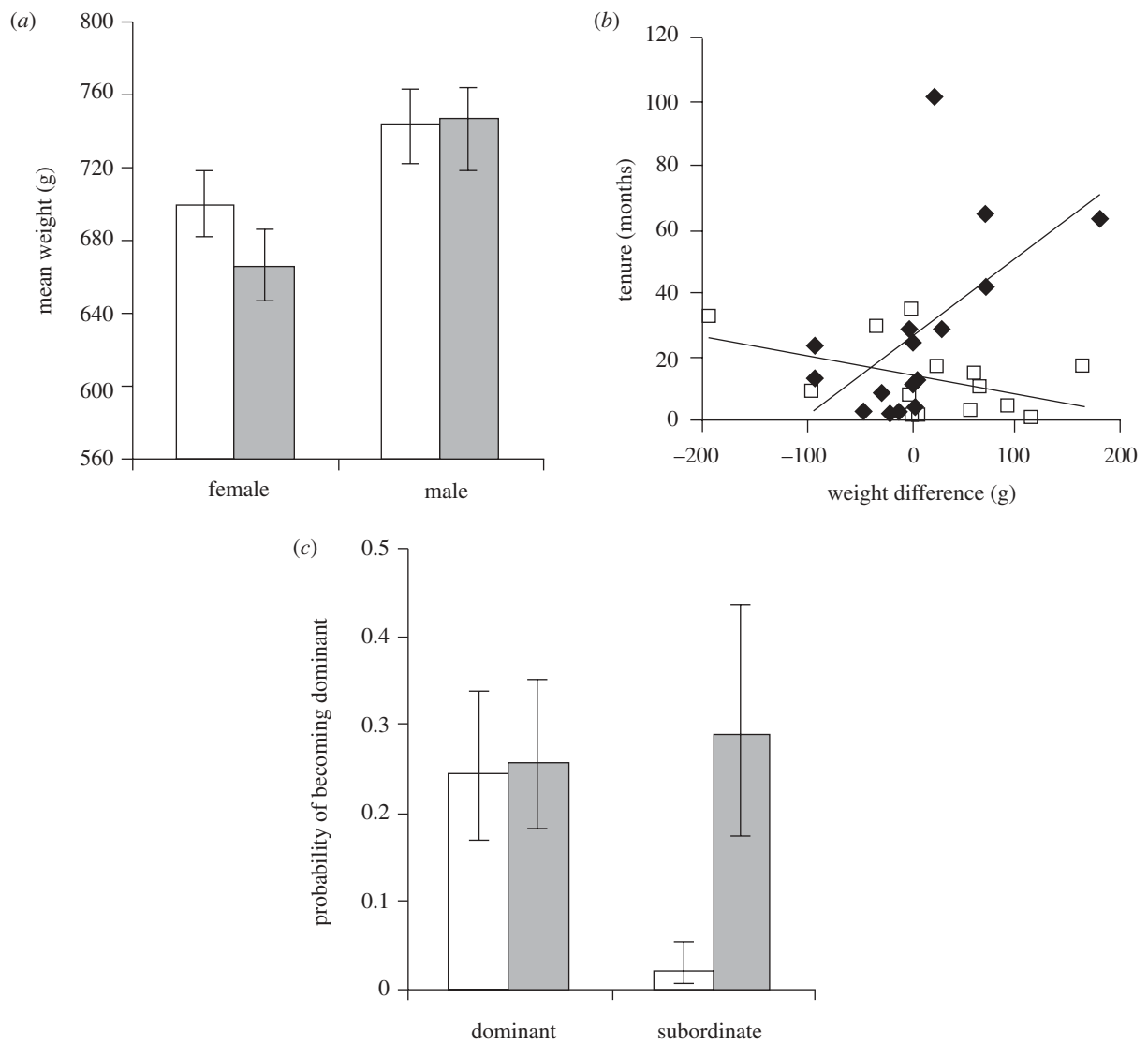


Figure 4. The acquisition and maintenance of dominant status in meerkats: (a) mean body mass in the three months before a dominance change of female and male meerkats that successfully (unfilled bar) acquired dominant status compared with a same-aged or older unsuccessful (filled bar) competitor; (b) tenure of the dominant position in female (filled diamonds) and male (open squares) helpers in relation to the difference in body weight between them and the oldest same sex subordinate in their group and (c) probability that daughters and sons born to dominant and subordinate mothers will acquire dominant status (unfilled bar, female; filled bar, male) (Clutton-Brock *et al.* 2006).

Damaraland mole-rats *Cryptomys damarensis* appear to be an exception and extra-group mating and multiple paternity within litters appear to be common (Burland *et al.* 2004).

Where dominant males monopolize access to a single breeding female, they usually do so for several seasons, generating large differences in breeding success between males as well as between females (figure 3c) and relatively high coefficients of relatedness between young born in successive litters. However, in meerkats and, possibly, in naked mole-rats, the reproductive tenure of dominant males is shorter than that of dominant females (figure 3b), so that reproductive skew and individual differences in breeding success are not as large as in females (figure 3d) and a higher proportion of males breed as dominants at some stage in their lifespans (Clutton-Brock *et al.* 2006) (M. J. O'Riain 2006, personal communication). Two separate mechanisms

may be responsible for the shorter tenure of males. First, breeding males whose partners die are often the father of all females in the group, including the new dominant female. 'Widowers' rarely guard or mate with related dominant females, play an enlarged role in guarding litters and leave their group to search for breeding opportunities in other groups while 'widows' invariably remain in their breeding group and so avoid the risks of dispersal (T. H. Clutton-Brock 2009, unpublished data). Second, breeding males, unlike breeding females, commonly face competition for their position from any related males that immigrated with them, as well as from unrelated immigrants from other groups. In contrast to breeding females, whose principal competitors are younger animals born in the same group, males have no opportunity to restrict the development of potential competitors or to evict them from the group before they become a serious threat to their position. This



argument also suggests a possible reason for the contrast in relative longevity between breeding females in cooperative and eusocial societies and males in polygynous species, where high reproductive skew is associated with a reduction in longevity (Clutton-Brock & Isvaran 2007). While dominant females in most cooperative and eusocial societies are usually able to minimize the risk of competition or challenge by suppressing the development of potential competitors or evicting them from the group, in most polygynous species males are not, with the result that high levels of reproductive skew are associated with frequent challenges for the breeding position and frequent, costly fights (Clutton-Brock *et al.* 1979).

## 8. DISCUSSION

As yet, the number of studies of cooperative mammals providing detailed information on the life histories and reproductive success of breeders and helpers in natural populations is small and generalizations are necessarily tenuous. However, it is clear that, across animal societies, cooperative breeding is closely associated with high levels of reproductive skew. In some societies (and possibly in most), simultaneous reproduction by other breeding females reduces the survival of offspring born to dominant females, favouring the suppression of breeding by other females and leading to high levels of reproductive skew in both sexes. Suppression of reproduction by subordinate females restricts their reproductive options and favours the evolution of nepotistic cooperation. Assistance in rearing young is associated with reductions in the fitness costs of breeding to dominant females and positive correlations between age and breeding success, strengthening selection pressures for longevity in breeders. Where helpers also provision breeding females, as in naked mole-rats, this can further reduce their extrinsic risk of mortality, leading to the evolution of unusually long lifespans in breeding females, which augment variance in breeding success among females and the degree of reproductive skew.

Variation in the life histories of breeders have profound consequences for the structure of vertebrate societies. In species where the mortality of breeding females is relatively high (as in many cooperative birds), subordinates have a substantial chance of acquiring breeding status outside their natal group. As a result, selection on subordinates is likely to favour dispersal, helpers are unlikely to remain for more than one or two seasons in their natal group, group size is relatively small and breeders are forced to contribute to rearing their own young. In these societies, selection pressures operating on helpers and breeders are relatively similar and differences in behaviour, physiology and anatomy between them are usually relatively small. At the other extreme are animal societies where mortality of breeders is relatively low, subordinates have little chance of acquiring breeding status outside their natal group, selection on subordinates favours philopatry and (if dominant females allow subordinates to remain) groups can be large. Under these conditions, selection on subordinates is likely to favour strategies adapted to raising

indirect components of their fitness by assisting related breeders and specializations for helping are likely to evolve, including adaptations in behaviour, reproductive physiology and growth. Increases in the number and specialization of helpers raise the potential reproductive rate of breeders, generating selection pressures on breeders to increase their fecundity, to improve their control of the behaviour and development of other group members and to extend their lifespans, which, in turn, reinforce selection pressures favouring indirect reproduction in subordinates.

This explanation of cooperative societies suggests that contrasts in colony or group size (and associated differences in the degree of reproductive skew) may help to account for contrasts in complexity. Specialized, eusocial societies are probably more widespread in insects than in vertebrates because the number of individuals per colony is so large that the *per capita* chances that an individual will occupy the breeding role are extremely low (Alexander *et al.* 1991; Bourke 1999). Obligate sterility and specialized, eusocial societies may be absent in cooperative vertebrates because the larger body size and greater energetic requirements of individuals restricts the potential size of groups, limiting the extent of divergence in the selection pressures operating on helpers and breeders (see Boomsma 2009). As would be expected, the most specialized cooperative societies found among vertebrates occur in herbivorous rodents of relatively small body size where the distribution of their food supply and the energetic requirements of individuals permit the formation of relatively large groups (Alexander *et al.* 1991; Bennett & Faulkes 2000; Faulkes & Bennett 2007). Similarly, among the carnivores, the most specialized cooperative societies occur in diurnal insectivores of relatively small body size, where heavy predation pressure favours the formation of large groups. In contrast, group size is comparatively small in most cooperative birds, which may explain why no species show a degree of specialization in cooperative breeding comparable to that of naked mole-rats (Russell 2004; Clutton-Brock 2006).

There are probably several reasons for the evolution of extended lifespans in breeding females in cooperative and eusocial species. In many of these species (including naked mole-rats), breeding females are routinely provisioned by other group members and this is likely to reduce extrinsic mortality associated with independent foraging (Alexander *et al.* 1991; Sherman & Jarvis 2002). Cooperative rearing may also reduce the survival costs of breeding to dominant females (Creel & Creel 2001; Clutton-Brock *et al.* 2006). Finally, increases in the annual reproductive success of breeding females throughout much of their period of tenure are common in cooperative species (Woolfenden & Fitzpatrick 1984; Creel & Creel 2001; Hodge *et al.* 2008) and are likely to favour the evolution of long breeding lifespans (Sherman & Jarvis 2002). A similar association between unusually long lifespans in breeding females and age-related increases in body size, fecundity and survival ('negative senescence') has been documented in a number of fish showing indeterminate growth (Vaupel *et al.* 2004).

This brief review of the evolution of cooperative behaviour provides a basis for assessing suggestions

that cooperation is best interpreted as a group-level adaptation maintained by group selection (Wilson & Wilson 2007). There is no question that the actions of individuals commonly affect the fitness of other group members and can generate variation in breeding success or survival between groups. For example, in polygynous societies, the eviction of other males by one dominant male may (conceivably) enhance the resources available for females, generating increases in the fitness of members of one-male groups. Similarly, it is possible that the monopolization of reproduction by a single dominant female in cooperative breeders reduces interference between females and increases recruitment in groups where subordinate females are suppressed. However, in both these cases, the behaviour of dominant individuals is likely to increase their own reproductive success and effects on the fitness of other group members may be unselected by-products of the adaptive strategies of individuals. While it is more tempting to view cooperative behaviour and its consequences (group territoriality, the construction of nests or burrows and the cooperative rearing of young) as group-level adaptations, here, too, there is no need to interpret them in this way. In many cooperative societies, the selfish strategies of individuals constrain opportunities for direct reproduction among subordinates to such an extent that maximizing the indirect component of their inclusive fitness represents an individual's optimal strategy (see Ratnieks & Helanterä 2009). Although it is possible to argue that activities that increase the fitness of multiple relatives represent a form of group selection, where groups consist of related individuals, the distinction between group selection and kin selection is semantic (West *et al.* 2007a,b,c; Gardner & Grafen 2009). In the relatively small number of cases where stable groups consist of unrelated individuals, cooperation is seldom strongly developed and, where it does occur, is either coerced by dominant group members or increases the fitness of cooperators.

The ultimate test of evolutionary explanations of social behaviour is whether they extend our understanding of variation in the behaviour of individuals and the structure of groups, either within or between species. In a previous review of mammalian societies, Kitchen & Packer (1999) tried to envisage a scenario where mammalian societies had evolved through evolutionary processes dominated by group selection and the activities of group members were adapted to maximizing benefits to the group. Competition between individuals should be minimal, reproductive interference and enforced evictions should be rare, cooperation between unrelated individuals should be common and birth sex ratios should be strongly biased towards females. This is a deeply unfamiliar picture to anyone acquainted with non-human mammals: in most social mammals, competition between group members is intense, reproductive interference is common, the more costly forms of cooperation are confined to relatives, average primary sex ratios are close to parity and the structure of societies appears to be a consequence of the attempts of individuals to maximize their inclusive fitness (Russell 2004; Clutton-Brock 2006). While this argument does not exclude the possibility that group

selection plays some role in maintaining cooperative behaviour, it suggests that, as in polygynous societies, the reproductive strategies of individuals in cooperative animals are best interpreted as attempts to maximize their inclusive fitness (see Grafen 2009). In this respect, the societies of non-human mammals differ from human societies, where accepted group norms commonly constrain the capacity of individuals to maximize their fitness at a cost to other group members, unrelated individuals often cooperate with each other, teamwork is frequently highly developed and extreme self-sacrifice is not uncommon (Bowles & Gintis 2003; Richerson *et al.* 2003; Boyd & Richerson 2009).

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