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Social competition and its consequences in female mammals

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Social competition and its consequences in female mammals

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Abstract

Although competition between females is one of the cornerstones of the theory of natural selection, most studies of reproductive competition have focussed principally on mating competition in males. Here, we summarise our current understanding of adaptive tactics used by competing females in social mammals, and assess the social mechanisms affecting competitive success and the evolutionary consequences of social competition between females. As well as emphasising the importance of female-female competition in social evolution, recent studies highlight the qualitative similarities in the operation of selection in females and males.

Introduction

Although competition between females is one of the cornerstones of the theory of natural selection, detailed studies of breeding competition have focussed largely on males (Darwin 1871, Andersson 1994). Compared to competition between males, female competition less frequently involves escalated contests and is less often associated with the evolution of exaggerated secondary sexual characters. Moreover, individual differences in breeding success among females are less obvious than among males: whereas measures of breeding success across a single season are sufficient to reveal large individual differences among males and to show that these are related to competitive ability, it is usually necessary to monitor the success of females over several breeding attempts to appreciate the magnitude of individual differences and to identify their causes (Clutton-Brock 1983). As a result, only after long-term studies of individual life histories became available was it possible to assess the magnitude and consistency of individual differences in reproductive success and to measure the strength of selection operating on females in iteroparous organisms (Clutton-Brock 1988).

One of the consequences of delays in associating the extent of variation in female fitness and the factors that affect it was the perception that competition between females is weaker than between males, and that females compete principally for resources while males compete principally for females (Emlen & Oring 1977, Clutton-Brock & Harvey 1978c, Clutton-BrockAlbon & Guinness 1989, TobiasMontgomerie & Lyon 2012). However, as more extensive studies of female life-histories have become available, they have shown that the extent of individual differences in reproductive success among females and the intensity of intrasexual competition to breed can be as great or greater than in males (Hauber & Lacey 2005, Clutton-Brock 2009c) and have emphasised the qualitative similarities in the selection pressures operating on both sexes (Clutton-Brock 2007).

As many previous reviews have emphasised, the high energetic demands of gestation and lactation in female mammals mean that the reproductive success of females is often constrained by the availability of resources and females often compete directly for food, threatening or attacking other individuals that feed close to them or for access to feeding territories (Kaufman 1983, Hoogland 1995a, Silk 2007a, Clutton-Brock 2009a, Stockley & Bro-Jorgensen 2011). Some of the best evidence of the effects of resource competition on females comes from studies of the effects of increasing group size, which commonly depress fecundity and increase mortality of females and their offspring (Clutton-BrockAlbon & Guinness 1982, Clutton-Brock 2002, Clutton-BrockHodge & Flower 2008, van Schaik *et al.* 1983, Silk 2007a, Clutton-Brock 2009b). Very similar patterns of resource competition occur in males, where breeding activity can also have high energetic costs (Lane *et al.* 2010), and individuals compete both for direct access to resources and for access to feeding territories (Clutton-Brock 2007), and survival is often sensitive to food shortages (Clutton-BrockMajor & Guinness 1985).

As well as competing for access to resources, females, like males, often compete to breed and, as in males, the structure of social groups intensifies conflicts of interest between group members (West-Eberhard 1983, West-Eberhard 1984). In some mammals, females compete to become sexually mature and, in extreme cases, one female suppresses the sexual development of all other females, evicting individuals that attempt to breed (Creel & Creel 2002, Clutton-Brock *et al.* 2006, Clutton-Brock 2009b). In others, females compete for access to mates, even though Operational Sex Ratios (the ratio of males to females that are ready to mate at a given time) are biased towards males. For example, in some ungulates where males defend groups of females during a well-defined mating season, there is often more than one receptive female in a male's harem on the same day, and females commonly compete for the attentions of males (Bro-Jørgensen 2002, Bro-Jørgensen 2011). Female competition may help females to ensure that they are mated by one or more males within the time frame of their reproductive cycles (Parker & Ball 2005), for the sperm supplies of successful males can become depleted (Dewsbury 1982, Preston *et al.* 2001, WedellGage & Parker 2002) or popular males may strategically conserve sperm for subsequent mating opportunities (Parker *et al.* 1996, WedellGage & Parker 2002). As would be expected, the frequency of overt female competition for mating partners increases in populations where adult sex ratios are strongly biased towards females (Milner-Gulland *et al.* 2003, CheneySilk & Seyfarth 2012), where there is a high degree of reproductive synchrony (Emlen & Oring 1977, Stockley & Bro-Jorgensen 2011), or where females mate with multiple partners (Charlat *et al.* 2007). In some species, the frequency of aggression received by subordinate females from dominants rises when they are in oestrus or are attempting to mate. For example, in chacma baboons, mate-guarded females face more aggression than sexually receptive females that are not mate-guarded and aggression between females is most frequent at times when there are multiple swollen females in the troop (Huchard & Cowlishaw 2011). This seldom appears to be caused by direct competition for access to males and another explanation is that females are attempting to prevent potential competitors from breeding (Stockley & Bro-Jorgensen 2011).

In group-living species, females also compete to raise offspring, to protect offspring access to resources and establish their status within the group, or to prevent them being evicted by other females (Clutton-Brock 1991, Stockley & Bro-Jorgensen 2011). Competition of this kind, which often involves individuals from different matrilines, is particularly intense in plural breeders that live in stable groups in well-defined home ranges or territories, including many of the baboons and macaques, spotted hyenas and some of the ground-dwelling sciurids. In several of these species, the size of matrilineal groups affects their relative dominance and breeding success and female members of dominant matrilines are frequently aggressive to female recruits born in subordinate matrilines, who represent potential competitors (Silk *et al.* 1981, SmaleFrank & Holekamp 1993).

This paper examines social competition in social mammals and describes the competitive strategies used by females and their ecological and evolutionary consequences. Section 2 describes the tactics used by females in competitive interactions; section 3 describes relationships between competitors, the role of dominance and the factors affecting the acquisition of rank; and section 4 explores some of the consequences of female competition.

Competitive tactics

Fighting

Fighting between female mammals is not uncommon, though it is usually less frequent than between males. In singular breeders, where reproductive skew is unusually large, adult females commonly fight over access to breeding territories (Fernandez-Duque 2009, pers.comm) while, in plural breeders, females occasionally fight when important resources are at stake: for example, female prairie dogs can fight for access to breeding burrows (Hoogland 1995a) and female ring-tailed lemurs take a leading role in territorial fights (Jolly & Pride 1999). Similarly, fights occur when females attempt to evict other females (or their offspring) from breeding groups, as in howler monkeys (Crockett 1984) and in banded mongooses (Cant, Otali & Mwanguha 2001, Cant 2010). In singular cooperative breeders, the death of the breeding female is often followed by intense fighting between her daughters and the death or eviction of unsuccessful competitors (Clutton-Brock *et al*. 2006, Sharp & Clutton-Brock 2011). In some mammals where competition between females is particularly intense, like meerkats (Clutton-Brock et al. 2006) and spotted hyenas (Holekamp and Swale, 2000), increased levels of competition between females can extend back into adolescence and early development. For example, in meerkats, competitive interactions between adolescents are more frequent between females than between males (Clutton-Brock 2009b) while, in spotted hyenas, siblicide (which occurs when resources are at short supply) is more frequent between females than between males or litters of mixed sex (James & Hofer 1999, Hofer & East 1997, 2008).

As yet, detailed studies of fighting tactics have been almost totally confined to studies of males. However, accounts of fights between females suggest that their distribution and duration coincide with the predictions of theoretical models: fights appear to be most frequent and intense where the benefits of winning or the costs of losing are large, and longest when the Resource Holding Power (or RHP) (Parker 1974) of contestants is approximately similar. There are probably several reasons why physical attacks are usually less frequent and less intense in females than in males (Andersson 1980). First, the fitness benefits associated with the resources at stake are greater in males than in females, as a consequence of both increased variance in reproductive success and of contrasts in Bateman gradients (Kokko, Klug & Jennions 2012). Second, a lesser number of individuals commonly compete simultaneously for the same resources as a result of biases in the Operational Sex Ratio (Emlen & Oring 1977). Third, risks associated with escalated fights may frequently be higher for females than for males, as they may entail fatal injuries for dependent offspring: for example, territorial fights among females frequently result in infant deaths in ring-tailed lemurs (Jolly *et al.* 2000) and, in several species, lactating females rarely engage in aggressive interactions (Wasser & Starling 1988, Huchard & Cowlishaw 2011). Finally, as a result of female philopatry, females are frequently competing with relatives whereas males are typically competing with unrelated individuals. In addition, philopatry can allow females to control the presence or development of potential rivals, so that threats between individuals of approximately equal RHP are less common than among males (Clutton-Brock 2009b, Clutton-Brock *et al.* 2010).

Threats, punishment and harassment

While conflicts between females sometimes lead to direct fighting, the majority of aggressive interactions between group members involve threats rather than physical attacks (Andersson 1980). For example, in studies of vervet monkeys, although maternal interventions occurred in less than 4% of juvenile interactions, maternal dominance rank predicted the outcome of up to 85.5% of all dyadic aggressive interactions between juveniles and 94.1% of those interactions that occurred in the presence of the juveniles' mothers, suggesting that the threat of maternal intervention was primarily responsible for controlling the acquisition of offspring rank (Horrocks & Hunte 1983). Threats allow individuals to modify the behaviour of potential competitors without incurring the costs and risks associated with escalated fights (Maynard Smith 1974) but are only likely to be effective where threatening individuals have the capacity to inflict costs on others sufficiently large to inhibit their behaviour (Parker 1974, Andersson 1980, Cant & Johnstone 2009).

In many societies, dominant individuals also punish subordinates that infringe their interests, inflicting fitness costs that offset the benefits of repeating the same behaviour. Where there are large asymmetries in power or dominance rank between individuals, the costs of punishing are often very low while costs inflicted on victims can be extremely high so that punishment is likely to be an evolutionary stable strategy (Clutton-Brock & Parker 1995a). Punishing tactics may be used to reduce the incidence of feeding competition by subordinates, to constrain their access to social partners or to coerce them into cooperative behaviour (Hauser 1992, Reeve 1992). Subordinates that repeatedly infringe the interests of the same dominant individual may receive progressively larger punishments and may, eventually, b evicted from the group or even killed (Clutton-Brock & Parker 1995a). However, while anecdotal examples of punishment are common, experimental evidence of the benefits of punishing tactics to the punisher are rare in wild animals.

One of the few examples of the consequences of punishment yet available is provided by experiments with cleaner wrasse, which involved presenting a dominant and a subordinate with a choice of two foods, one preferred and one less preferred, which were immediately reversed if the subordinate began feeding on the preferred food (RaihaniGrutter & Bshary 2010). After repeated trials, dominants learned to attack subordinates if they began to eat the preferred food and subordinates learned to avoid this choice. The fact that fish are capable of learning to avoid choices that incur punishment by dominants suggests most mammals are likely to be capable of similar learning processes and that punishing tactics are often likely to increase the fitness of dominants.

Conflicts of interest between group members also lead to regular harassment. For example, where two females are competing for divisible resources, repeated attempts to gain access by subordinate competitors may eventually raise the costs of continued defence to dominants until they reach a point where the net benefits of maintaining exclusive access are lower than the costs of defence. Situations of this kind resemble a ‘war of attrition’ where the winner is the individual that can afford to persist for the longest time (Clutton-Brock & Parker 1995b). Persistent harassment can occur in a variety of circumstances. In some societies, dominant females harass subordinates or their offspring, sometimes directing unprovoked threats or attacks at them which may raise glucocorticoid levels, sap the confidence of subordinates, discourage retaliatory attacks and, in extreme cases, cause them to leave the group (Dunbar & Dunbar 1977, Silk 2002, Stockley & Bro-Jorgensen 2011). Harassment is also often used by subordinates to modify the behaviour of dominants. For example, hungry individuals sometimes harass successful foragers or hunters for a share of the food that they have acquired and adolescents of either sex may harass copulating couples (Clutton-Brock & Harvey 1976, Clutton-Brock & Parker 1995b). More generally, the stress induced by social conflicts varies across species depending on the structure of societies as well as within societies depending on social dynamics, and may be higher in dominants than in subordinates when the costs of acquiring and maintaining dominance are very high (Goymann & Wingfield 2004, Rubenstein & Shen 2009).

Reproductive suppression

In many social mammals where females are philopatric, female group members (who are often close kin) compete with each other to breed and raise young (Clutton-Brock 2009b, Clutton-Brock & Lukas 2011). Regular aggression directed by dominant females at subordinates or their offspring is common, especially in species living in large groups, where average coefficients of relatedness are relatively low and females belonging to different kin groups compete with each other to breed and rear young. Competition between females often inhibits females from mating and can depress the fertility of subordinates, disrupting their reproductive cycles and causing them to down-regulate their reproductive systems (Wasser & Barash 1983, Young 2009). For example, in yellow baboons, dominant females direct frequent aggression at cycling subordinate females in the follicular phase and these attacks can increase the number of cycles before conception

(Wasser & Starling 1988), while in other species (including several rodents, some carnivores and almost all of the marmosets and tamarins) subordinates are temporarily infertile (Young 2009). As well as disrupting reproduction, regular aggression can lead to increased rates of abortion and reductions in juvenile survival (Silk 2007a, Stockley & Bro-Jorgensen 2011). For example, in hamsters, interactions between subordinate and dominant females shortly after mating increase implantation failures in subordinates, while interactions later in pregnancy lead to increased rates of foetal mortality (Huck 1988a,b). Studies of several species suggest that reproductive suppression intensifies when resources are limited and eases when they are abundant (Young 2009, Clutton-Brock *et al.* 2010). For example, in Damaraland mole-rats, physiological suppression of subordinate females is relaxed during the annual rains when ecological constraints are relaxed (Young *et al.* 2010) while, in meerkats, dominant females are more likely to tolerate subordinate reproduction when food is abundant (Clutton-Brock *et al*. 2010).

The physiological mechanisms underlying reproductive suppression vary between species and are still not well understood. Early studies suggested that reproductive suppression in subordinate females was caused by chronic elevation of glucocorticoid adrenal hormones as a result of social ‘stress’ induced by regular aggression from dominants (Wasser & Barash 1983). However, recent research has shown that the presence of dominant females, or cues signalling their presence, can, on their own, prevent subordinate females from mating or conceiving in the absence of direct interactions with dominant females (French 1997, Young 2009). For example, in naked mole-rats the presence of dominant females is sufficient to prevent subordinate females in coming into breeding condition (Faulkes *et al.*

1997) while proximity of dominant females is sufficient to inhibit mating in several primates (Overduin-de Vries *et al.* in press, TownsendDeschner & Zuberbuhler 2008). Moreover, in some species, cortisol levels do not vary consistently between subordinates and dominants (Abbott *et al.* 2002, Starling *et al.* 2010), while, in other species, subordinates show lower glucocorticoid levels than dominants (Creel 2001) and these results are commonly interpreted as evidence that glucocorticoid levels associated with aggression are not responsible for reproductive suppression. However, an alternative explanation is that the relationship between social status and glucocorticoid levels depends on the structure of societies and the relative costs of acquiring and maintaining dominance, as well as on the relative intensity and frequency of threats faced by subordinates from dominants (Goymann & Wingfield 2004, Rubenstein & Shen 2009). Dominants may exhibit higher cortisol levels than subordinates in species where maintaining dominance requires frequent physical contests, but not where dominance is inherited and stable as in female spotted hyenas. In addition, the physiological costs of social status can even vary within species, in relation to fluctuations in the level of social conflict. For example, reproductive suppression may be induced by substantial increases of glucocorticoid levels in subordinates at times where they are attempting to breed and are the target of frequent aggression by dominants (Young 2009).

Although the role of aggression in reproductive suppression has attracted most attention, it is clear that several other factors can be involved. In some species, the absence of unrelated breeding partners in the group commonly delays the sexual maturation of subordinates (Pettitt & Waterman 2011) and the replacement of related dominant males with unrelated males can cause subordinate females to up-regulate their reproductive systems and compete for the breeding role: for example, in Damaraland mole rats and meerkats, the death or removal of resident males causes previously suppressed subordinate females to up-regulate their reproductive systems and compete for the breeding role (Cooney & Bennett 2000, Clutton-Brock *et al.* 2001b). Other suggested reasons why it might benefit subordinates to defer breeding include reduced foraging skills and associated energetic constraints, negative effects of breeding at the same time as dominants on the fitness of their own offspring, and costs to indirect components of their fitness if dominants are close relatives (Young 2009).

Evidence of these effects has led to a debate over whether subordinate infertility should be interpreted as a consequence of constraints on subordinate breeding imposed by dominants or of voluntary restraint by subordinates caused by the need to avoid attracting aggression from dominants or by high costs of breeding associated with reduced condition or inferior foraging skills (Young 2009, Saltzman, Digby & al. 2009). However, the distinction between these arguments is not as clear as it may initially appear for that subordinates may commonly show restraint because dominants constrain their reproductive options (Young 2009). For example, subordinates may respond to the presence of dominants by down-regulating their reproduction (reproductive restraint) because dominants are likely to evict them if they attempt to breed, so that the likely fitness benefits of competing to breed are low (a reproductive constraint). Evidence that other factors modify the frequency of breeding by subordinates (such as condition or the absence of unrelated partners) does not necessarily argue for interpretations based on restraint, for effects of this kind would be expected under both scenarios. Perhaps the most realistic view is that subordinates commonly show restraint because dominants constrain their reproductive options (Young 2009).

Attempts by dominant females to prevent other females from breeding or to reduce their success in rearing offspring are sometimes regarded as examples of spite since they can occur at times when the benefits of reproductive suppression are not obvious or resources are abundant (Stockley & Bro-Jorgensen 2011). However, although this is theoretically possible (Gardner & West 2004), the fitness costs of attacks on subordinates and their offspring may often be low while simultaneous breeding by subordinates may often have long-term costs to dominants and their dependents (Clutton-Brock *et al.* 2010). Consequently, it is probably more realistic to regard attempts by dominants to suppress reproduction by subordinates as an example of selfish behaviour rather than spite.

Infanticide

While infanticide by females has attracted less attention than infanticide by males it is probably more widespread (Rödel *et al.* 2008) and frequently represents a threat for group-living females (Digby 2000). In some cases, it may be a coincidental consequence of rough handling of the offspring of subordinate females by dominants, or of repeated aggression affecting their access to resources and their condition and may, sometimes, lead to serious wounding or death (Muroyama & Thierry 1996, Kleindorfer & Wasser 2004, Lloyd & Rasa 1989). In others, dominant females kidnap offspring from subordinates without displaying any sign of aggression towards the kidnapped infant, and then restrain mothers from retrieving their infant until it dies from dehydration (Brain 1992, Digby 2000). However, especially in rodents and carnivores, infanticide can also occur as a result of direct, lethal attacks on juveniles born to other females (Hoogland 1985, Clutton-Brock *et al.* 1998b). As in males, heightened levels of circulating testosterone may play an important role in the control of infanticidal behaviour in females (Ebensperger 1998a, Ebensperger 1998b) and the incidence of attacks by pregnant females increases during the second half of the gestation period, at the same time as increases in circulating levels of testosterone (Ebensperger 1998a, Clutton-Brock *et al*. 1998b).

In some species, there is evidence that the incidence of infanticide is affected by the sex of infants. The clearest evidence of effects of this kind comes from societies where matrilineal female groups compete with each other within a larger group and the relative rank of matriline is related to their size, so that additional female recruits to competing matrilines represent a threat to competitors (Clutton-Brock 1991). For example, in captive groups of pigtail macaques, dominant females selectively target female juveniles born into low ranking matrilines, who show low survival compared either to the sons of subordinate mothers or to the daughters of mothers belonging to high ranking matrilines (Sackett 1981). One study has even produced evidence that subordinate females pregnant with female offspring are more likely to be wounded by other group members than those pregnant with males (Sackett 1981) though studies of natural populations have not yet confirmed this effect. Effects of regular aggression from other females are not restricted to primates and have been shown to affect the development or survival of offspring in many other plural breeders (Clutton-BrockAlbon & Guinness 1982, Hoogland 1995b, Silk 2007a, Digby 2000).

Infanticide can have several different benefits to dominant females (Hrdy 1979). In some cases, it may generate direct benefits from the consumption of infants while, in others, it may reduce the costs of maternal care directed at unrelated offspring (Digby 2000). For example, in northern elephant seals, pups separated from their mothers often attempt to suckle on other lactating females, which may then react by attacking the pup and attacks from females are responsible for the majority of infant deaths in this species (LeBoeuf & Briggs 1977). Infanticide commonly reduces immediate competition for space or resources between infanticidal mothers and other breeding females and their offspring (Wolff & Cicirello 1989, TuomiAgrell & Mappes 1997, Rödel et al. 2008). For example, in cooperative breeders, like meerkats, simultaneous breeding by more than one female reduces the ratio of helpers to pups and the growth of pups falls (Clutton-Brock *et al*. 2010) and evidence that infanticide is more likely in pregnant than non-pregnant females suggests that its function is partly to reduce competition for the killer's offspring (Clutton-Brock *et al*. 1998b). It may have additional benefits: victims of infanticide may subsequently contribute to suckling and rearing infants subsequently produced by infanticidal females as in marmosets (Digby 1995) and meerkats (Clutton-Brock *et al*. 1998b). Similarly, both the tendency for members of competing matrilines to target aggression on female recruits to subordinate matrilines (see above) and evidence that, in some species, competing groups search out and kill litters born to neighbouring groups suggests that it may often generate strategic benefits by limiting future resource competition or contributing to the maintenance of social status or territory (Digby 2000).

Eviction

In a substantial number of social mammals, competition between resident females leads to evictions or to groups splitting. In singular breeders, increasing aggression directed by dominant females at older subordinates often builds up until subordinates are chased out of the group by the dominant female. For example, in meerkats, dominant females evict (virtually) all female subordinates before they are four years old (Clutton-Brock *et al*. 2010). Eviction of subordinate females by dominants is also common in some plural breeders. For example, in red howler monkeys, high-ranking females frequently evict younger and lower-ranking females from their groups (Pope 2000) while, in banded mongooses, coalitions of older dominant females intermittently evict entire cohorts of younger females from their group (Gilchrist 2006, Cant 2010).

The timing of eviction within the breeding cycle also varies between species: for example in meerkats, dominant females commonly evict subordinates during the latter half of their (own) gestation period and allow them to return a few days after they have given birth (Clutton-Brock *et al*. 1998b, Young *et al*. 2006) while, in banded mongooses, younger females are often evicted at times when several group members are in oestrus (Gilchrist 2006).

Eviction commonly exposes emigrants to substantial risks and can raise cortisol levels and induce abortion in pregnant evictees (Young *et al*. 2006, Young 2009, Gilchrist 2006, Clutton-Brock 2009b). As a result, subordinates often seek to avoid or delay eviction. For example, subordinate female meerkats that are at risk of eviction engage in frequent submissive gestures and frequent attempts to groom dominant females (Kutsukake & Clutton-Brock 2006b) and experiments in which grooming frequency was experimentally reduced showed this increased rate of aggression (Madden & Clutton-Brock 2009).

The eviction of subordinate females can generate several different benefits to dominant females. In some cases, it probably serves to reduce competition for resources or removes potential competitors from breeding positions or high social rank (Clutton-Brock *et al*. 2006, Clutton-Brock 2009b). In others, it may reduce the risk of infanticide by other females. For example, in meerkats, pregnant females frequently kill infants born to other group members within 2-3 days of birth and breeding females often evict older subordinate females from the group in the weeks before parturition, allowing them to return after their pups are several days old (Clutton-Brock *et al.* 1998b). Eviction frequently induces abortion in evicted females and evicting older subordinates (who are more likely to have conceived) may reduce the risk that the dominant female's pups will be exposed to pregnant females. In addition, abortion increases the chances that subordinates will subsequently suckle pups born to the dominant female, so that an additional benefit of evicting subordinates to dominants may be that it increases contributions to rearing their pups (Young *et al*. 2006).

In plural breeders, rising levels of aggression between sub-groups of females in large groups can eventually cause groups to split, generating two or more separate groups with distinct home ranges. For example, in macaques, increases in group size commonly lead to increased competition between females which eventually lead to larger groups splitting and to reductions in competition for resources (Okamoto 2004). When groups split, they typically do so along matrilineal lines so that average levels of kinship between group members tend to increase. For example, when groups of yellow baboons split, females typically remain in the same sub-group as their close maternal kin (van Horn *et al.* 2007). Compared with evictions, the immediate costs of group splitting are relatively low since individuals are not forced to leave groups alone. However, it may have substantial deferred costs if one of the new groups is forced to occupy an inadequate range or is unable to compete effectively with neighbours but, as yet, few studies have been able to assess how large such effects may be.

Competitive relationships

Dominance systems

Where potential conflict or limited resources occur between individuals of contrasting fighting ability, less powerful individuals often benefit by avoiding conflict and allowing their opponents to monopolise resources without direct conflict (Bernstein 1981, Kaufman 1983). Subordinates commonly either avoid the proximity of dominants or adjust their behaviour to avoid conflict as soon as they are threatened and, as a result, a high proportion of potential conflicts between group members are usually resolved without fighting. Where there are consistent differences in fighting ability or power between individuals, the avoidance of conflict by weaker individuals generates hierarchies of dominance (or submission) between group members (Rowell 1974, Silk 1993). Although some early descriptions of dominance suggested that hierarchies were adaptations that benefited groups by reducing conflict between their members, a more likely interpretation is that they are non-adaptive consequences of attempts by individuals to avoid escalated conflicts that they are unlikely to win (Kaufman 1983, Clutton-Brock & Harvey 1976).

The frequency of interactions, the regularity of outcomes and the linearity of hierarchies all vary widely between and within species. In some species, there are well defined dominance hierarchies in both sexes and subordinate individuals seldom win encounters with competitors of higher rank, as in baboons or spotted hyenas (Silk 1993, East & Hofer 2010). In others, an individual's rank depends on location: for example, in red deer, the relative dominance of females is affected by whether or not they are within their usual range (Thouless & Guinness 1986).

Finally, in a few species, there is no regular pattern in the outcome of aggressive interactions between adult female group members. For example, lionesses commonly threaten pride-mates feeding on the same kill, but individuals are seldom displaced from their feeding sites and there are no marked differences in the frequency with which individuals give and receive threats (PackerPusey & Eberly 2001). Similarly, in Kalahari meerkats, foraging females usually respect each other's access to feeding sites and seldom contest access to feeding sites, though the most dominant female in each group occasionally displaces subordinates (Kutsukake & Clutton-Brock 2006a).

The reasons for variation in the consistency of dominance relationships between females are uncertain. Contrasts in the regularity and stability of hierarchies have been most extensively studied in primates (Rowell 1974, Bernstein 1981) where it has been suggested that the presence of strong linear hierarchies in females is associated with reliance on foods that are distributed in patches of high value and with intense direct competition between group members for resources (Wrangham 1980, SterckWatts & van Schaik 1997). Some intraspecific comparisons support this suggestion. For example, in one population of savannah baboons where resources were concentrated, competitive interactions were common, dominance relationships were well developed and affected rates of food intake while, in a second population where resources were widely dispersed, competitive interactions were less frequent and dominance relations were inconsistent and coalitions did not occur (Barton & Whiten 1993, BartonByrne & Whiten 1996). However, the quantitative comparisons of hierarchies across samples of populations which would be needed to test this prediction are not yet available (Clutton-Brock & Janson 2012).

It is also unclear whether there is any consistent association between the food distribution and hierarchical behaviour at the species level (Clutton-Brock & Janson 2012). Female hierarchies have been reported in herbivores as well as in carnivores and vary widely between species with similar diets (Clutton-BrockAlbon & Guinness 1982, Clutton-BrockAlbon & Guinness 1984, Clutton-Brock 2009c, Wells & von Goldschmidt-Rothschild 1979, Rubenstein & Nunez 2009). For example, while they are weak or absent in lionesses (PackerPusey & Eberly 2001), they are well developed in spotted hyenas (HolekampSmale & Szykman 1996, East *et al.* 2010). Among primates, there are no obvious differences in the frequency with which linear dominance hierarchies have been reported between species allocated to dietetic groupings and there are marked interspecific contrasts in the prominence of hierarchies which do not appear to be correlated with obvious differences in ecology (Clutton-Brock & Janson 2012). For example, among macaques, the structure and regularity of dominance hierarchies differs between species and is not obviously associated with variation in ecology (Thierry 1990, Menard 2004) while in lemurs, similar patterns of social structure are found in species with contrasting feeding ecology (Kappeler 1997). One recent suggestion is that contrasts in the extent to which females tolerate each other in macaques are associated with attacks in paternal relatedness and reproductive skew in males (Schülke & Ostner 2008, Schülke & Ostner 2012).

Dominance and reproductive success

As longitudinal records of female breeding success have become available, an increasing number of studies have demonstrated positive correlations between dominance and breeding success in females (Clutton-BrockAlbon & Guinness 1982, Altmann & Alberts 2003, Stockley & Bro-Jorgensen 2011). For example, in spotted hyenas, high ranking females have priority of access at kills, breed at younger ages than subordinates, wean their offspring more rapidly, breed more frequently and produce more surviving offspring (HolekampSmale & Szykman 1996, Holekamp & Dloniak 2009, East et al. 2010). Studies of several primates also show that high-ranking females have priority of access to resources (Barton & Whiten 1993, Holand *et al.* 2004) breed earlier and more frequently (Bulger & Hamilton 1987, Smuts & Nicolson 1989, Barton & Whiten 1993, Wasser *et al.* 1998, Altmann & Alberts 2003, Setchell *et al.* 2002, Packer *et al.* 1995) and their infants grow faster (Packer *et al*. 1995, Johnson 2003, Altmann & Alberts 2003) and are more likely to survive their first year of life (PuseyWilliams & Goodall 1997, Altmann & Alberts 2003, Wasser *et al.* 2004) compared to the offspring of subordinate females. In addition, maternal rank can affect a female's access to dominant males and to effective paternal care: for example, in baboons, lactating females compete to maintain proximity to an adult male "friend" whose presence limits infanticide risk (PalombitCheney & Seyfarth 2001). Positive correlations between female dominance and breeding success are not confined to species living in stable groups and have also been found in species that live in open groups, including elephants (Lee 2011) and red deer (Clutton-BrockAlbon & Guinness 1984, Clutton-BrockAlbon & Guinness 1986, Clutton-BrockAlbon & Guinness 1988).

As well as affecting breeding success, dominance can affect the extent to which individuals are exposed to the risk of predation and their relative rates of survival (Silk *et al.* 2010). For example, both in long-tailed macaques and baboons, high-ranking females are more likely than subordinates to maintain safe, central positions in the group where they are less exposed to predators (van Noordwijk &

van Schaik 1987, RonHenzi & Motro 1996). Similarly, in naked mole-rats, dominants are seldom exposed to the risks of foraging independently or of protecting burrows against intruders (Lacey & Sherman 1991). As a result of their priority of access to resources, dominants may also show lower parasite loads and rates of infection. For example, a recent study of male baboons further shows that high social status is positively associated with fast wound healing in male baboons (ArchieAltmann & Alberts 2012).

Although a substantial number of studies have found positive correlations between dominance and breeding success or survival, this is not always the case (AltmannHausfater & Altmann 1988, Silk 1993). Abundant food supplies or severe food shortage can both mask the influence of social rank (Woodroffe & Macdonald 1995, Cheney *et al.* 2004). For example, studies of provisioned groups of Japanese macaques found no association between female dominance and breeding success (GouzoulesGouzoules & Fedigan 1982). Conversely, a study of a declining population of yellow baboons found no association between dominance and breeding success (Wasser *et al.* 2004). Group size can also be important: for example, one study of ring-tailed lemurs found that positive correlations between dominance and breeding success were restricted to large groups (Takahata *et al.* 2008).

The acquisition of dominance

Where female dominance and breeding success are correlated, strong selection pressures are likely to favour the acquisition of high status by females. As in males, a variety of factors can affect the probability of acquiring high social rank. In many species, female dominance is closely related to age and age-related dominance relations have been demonstrated in a wide range of mammals, including feral ponies (Rutberg & Greenberg 1990), African elephants (Archie *et al.* 2006), mountain goats (Cote 2000), meerkats (Clutton-Brock *et al*. 2006), chimpanzees (PuseyWilliams & Goodall 1997) and bottlenose dolphins (Samuels & Gifford 1997). In several species, including ponies and elephants, dominance status is also associated with body mass (Rutberg & Greenberg 1990, Archie *et al*. 2006). Though this could be a consequence rather than a cause of high status, experiments with house mice show that body mass before introduction predicts subsequent dominance rank (Rusu & Krackow 2004).

Androgen levels may also affect the aggressiveness of females and their acquisition of dominant status (Staub & de Beer 1997). Although, within species, relationships between dominance status and androgen levels are often inconsistent (AltmannSapolsky & Licht 1995, von EngelhardtKappeler & Heistermann 2000, KorenModady & Geffen 2006), in several species where female competition is intense (including meerkats, spotted hyenas and several social lemurs) dominant females show elevated levels of aggression and of circulating testosterone during the latter half of gestation (DloniakFrench & Holekamp 2006, Drea 2007, Clutton-Brock 2007, Clutton-Brock 2009c).

A variety of developmental factors can affect the chance that females will acquire and maintain high status. The birth weight and subsequent growth rates of juveniles often affect their relative rank and these differences are frequently maintained into adulthood (Clutton-Brock 1991, Clutton-Brock *et al*. 2006). As a result, environmental and social factors that influence the growth and development of juveniles can also have an important influence on their probability of acquiring high rank as adults (Clutton-Brock 1991, Alonso-Alvarez & Velando 2012).

Where female rank affects resource access it can also affect condition with the result that dominant females produce heavier offspring that grow faster and are likely to acquire higher rank themselves. For example, in spotted hyenas, the offspring of dominant females have higher circulating levels of insulin-like growth factor (IGF-1), grow faster and are both more likely to survive and to breed successfully than those of subordinate mothers (Holekamp & Dloniak 2009, Ho□ner *et al.* 2010). Similarly, in Kalahari meerkats, dominant females are able to displace subordinates from feeding sites and gain more weight each day while their daughters are heavier at birth, grow faster and are more likely to acquire dominant status as adults than those of subordinates (Clutton-Brock *et al*. 2006). Variation in hormone levels associated with maternal status can also affect the development of offspring. Rank-related differences in the mother's hormonal status during pregnancy have been shown to affect foetal development in spotted hyenas: dominant females have higher androgen levels during the second half of gestation and cubs born to mothers with high androgen levels during pregnancy are more aggressive towards other cubs and mount them more frequently than cubs born to mothers with low androgen levels (DloniakFrench & Holekamp 2006).

Dependent rank

In contrast to males, whose rank often depends on physical strength and fighting ability (van Noordwijk & Van Schaik 2004), the acquisition and maintenance of rank in females is often dependent on their capacity to secure social support from other group members (Kapsalis 2004, Silk 2009). 'Dependant' rank systems, where the status of individuals is strongly influenced by the rank of their matrilineal group, have been documented in carnivores (Holekamp & Dloniak

2009, East & Hofer 2010) and are common in cercopithecines (Kapsalis 2004, Chapais 2004) though they do not occur in all social primates (SautherSussman & Gould 1999, Perry *et al.* 2008).

The most detailed descriptions of dependant rank systems come from studies of baboons and macaques, where mothers support their daughters in competitive interactions against the offspring of other females and maternal support helps to establish the rank of daughters in their group (HausfaterAltmann & Altmann 1982, Chapais 1988, Chapais 2004, SilkAltmann & Alberts 2006a, Maestripieri 2011). For example, in Japanese macaques, females that behave submissively to dominant peers when their mother is absent can outrank them if their mother is present and has recently intervened in interactions on their behalf (Chapais 1988, Chapais 2004). As a result of maternal intervention, juvenile or adolescent females whose mothers have died or dispersed from their natal group often fail to acquire high rank as adults (Walters 1980, Johnson 1987).

Associations between maternal rank and breeding success, and the rank and breeding success of their daughters raise important questions about the relative importance of social, environmental and genetic factors affecting female status which have not yet been answered. The available evidence suggests that all three are commonly involved, though their relative importance may differ between species. For example, selection experiments with captive rodents have demonstrated genetic variance for dominance (Moore *et al.* 2002, Wilson *et al.* 2009). Similarly, a quantitative analysis of dominance interactions between wild female red deer using a multi-generational genetic pedigree suggests that dominance is partly heritable (Wilson *et al.* 2011). In contrast, in spotted hyenas, females sometimes adopt cubs born to other members of their clan and long-term data show that their rank as adults depends on the rank of their surrogate mother not on that of their genetic mother (East et al. 2010, East & Hofer 2010). Since social and genetic factors can interact to induce heritable changes in patterns of gene expression, it is also possible that epigenetic mechanisms play an important role in mediating trans-generational inheritance of social status (Champagne & Curley 2009).

Although the relative rank of females often increases with their age, where females live in large, stable groups (as in many of the baboons and macaques as well as spotted hyenas), mothers commonly support their younger daughters against older sibs and this establishes inverse relationships between age and relative rank among female siblings which often persist after the mother's death (HolekampSmale & Szykman 1996, Chapais 2004, East et al. 2010). As yet, data suggest that 'youngest ascendancy' rules of this kind may be restricted to societies where females live in groups that include several competing matrilines, like savannah baboons and spotted hyenas, although it is not clear why this should be the case, several different benefits to mothers of supporting younger siblings over older have been suggested. For example, mothers may support younger offspring against their older sibs because this helps to protect them from competition that might threaten their survival or eventual breeding success. Alternatively, by constraining the status of older daughters, matriarchs may reduce the risk that coalitions of their older daughters will attempt to displace them (Horrocks & Hunte 1983).

Where groups include several competing matrilines, adolescent females often receive support from their sisters and other matrilineal relatives as well as from their mothers. Individuals belonging to relatively high-ranking matrilines benefit from having larger numbers of high-ranking relatives who are more socially active and can help to induce submission in competitors more effectively (Pereira 1992, Chapais 1992, Chapais 2004) with the result that they commonly show faster growth, higher survival, acquire higher status and have higher fitness than those belonging to low ranking matrilines (Silk 2007a, Silk 2009). In some species, the relative rank of matrilineal groups is associated with their size while, in others, it appears to be determined by the dominance of the group's matriarch (Silk 2007a, Silk 2009, Clutton-Brock 2009b).

Long-term studies of primates have documented the relative frequency of support given to different categories of relatives and their effects. In general, females are most likely to support close female kin and preferential treatment is extended to mothers, offspring, grandmothers, grand-offspring and, in some cases, to aunts and nieces - but seldom to more distant relatives, where coefficients of relatedness are below 0.25 (Kapsalis & Berman 1996, Berman & Chapais 2004, Silk 2009). As yet, it is unclear whether this threshold is a consequence of constraints on the ability to recognise kin or occurs because it becomes more difficult to satisfy the requirements of Hamilton's rule as relatedness declines. Experiments with Japanese macaques show that sisters, grandmothers and great-grandmothers are able to influence rank acquisition by immature females, while aunts, grand-aunts and cousins rarely do so (Chapais 2001, Chapais 2004).

Recent studies of baboons and macaques also suggest that patrilineal kinship can affect supportive relationships, though effects are usually weaker than those of matrilineal kinship (Silk 2007a, Silk 2009, Widdig 2007). For example, in baboons, fathers support their offspring in conflicts with other juveniles (Buchan *et al.* 2003) and females form stronger bonds with their paternal half-sisters than with unrelated individuals if they have few maternal kin in the group (SilkAltmann & Alberts 2006a, SilkAlberts & Altmann 2006b). Similarly, in Rhesus macaques, females affiliate more with paternal half-sisters and avoid intervening against them (Widdig *et al.* 2001, Widdig *et al.* 2006) while, in mandrills, juveniles have closer relationships with paternal half-sibs than with unrelated adults (Charpentier *et al.* 2007). However, paternal kinship does not affect the strength of social bonds in all species: for example, white-faced capuchins show no tendency to give preferential treatment to paternal half-sibs over unrelated individuals (Perry *et al*. 2008).

Kinship and competition

Kin selection theory suggests that competition between close relatives should be less intense than between unrelated females (Hamilton 1964) and a wide range of studies have investigated whether or not this is the case. Their results show a widespread tendency for females to be more tolerant and supportive of close kin, though this is by no means universal and they will also engage in lethal fights with competing relatives or kill their young (Hoogland 1995b, Stockley & Bro-Jorgensen 2011, McCormick *et al.* 2011). As the previous section describes, female kin commonly associate with and support each other in many plural breeders where groups include a mixture of close relatives and distantly related females. In addition, there is extensive evidence of increased tolerance of kin in species where breeding females occupy independent ranges. For example, in voles, females show a preference for settling close to relatives and individuals with ranges close to kin breed earlier (Pusenius *et al.* 1998), rear more offspring and show higher rates of survival in the next breeding season (Lambin & Krebs 1993, Lambin & Yoccoz 1998) than individuals with ranges close to non-kin. In Alpine marmots, infants are more likely to survive their first winter in hibernation groups consisting largely of close relatives than in groups where most individuals are not closely related (Arnold 1990a, Arnold 1990b) and the breeding success of dominant females is depressed by the number of unrelated subordinate females in the group but not by the number of daughters present (HacklanderMostl & Arnold 2003). In some cases, the probability that subordinates will be evicted is affected by their relatedness to the dominant female. For example, in meerkats, the probability that a female will be evicted increases as her coefficient of relatedness to the dominant females falls (Clutton-Brock et al. 2010). However, this is not the case in other mammal species: for example, in red-fronted lemurs, the probability that females will be evicted depends primarily on the size of their group and is not related to their kinship to other group members (Kappeler & Fichtel 2011).

Several studies have investigated whether infanticidal attacks are more likely to be directed at unrelated subordinates than at close relatives. Here, too, results are mixed. In some cases, females usually kill young that are unrelated or distantly related to them. For example, in Belding's ground squirrels, infanticidal females are usually distant relatives or unrelated to the young they kill (Sherman 1981) while, in bank voles, familiarity between females decreases their tendency to kill each other's offspring (YlonenKoskela & Mappes 1997). In other species, females are more likely to attack the offspring of subordinate competitors, whether they are related or not. Some of the best evidence comes from studies of black-tailed prairie dogs, where breeding females commonly kill litters born to other females belonging to the same social group (Hoogland 1985, Hoogland 1995b). Mothers whose pups are killed typically occupy nursery burrows close to the killers and are smaller and lighter than their neighbours and, in many cases, are close relatives of the females that attack them. Similarly, in meerkats and marmosets, dominant females that are pregnant commonly kill the newborn offspring of subordinate females that give birth in the group, which would otherwise be heavier than their own future offspring (Clutton-Brock *et al*. 1998b, Young & Clutton-Brock 2006, Saltzman *et al.* 2009). In meerkats, subordinate females are commonly the daughters of dominants, so that dominant females frequently kill their own grand-offspring (Clutton-Brock *et al*. 1998b, Young *et al.* 2006).

Consequences of female competition

The regulation of female group size

Competition between females for resources and reproductive opportunities has important consequences for their ecology and evolution. Where resources are sparse or clumped in small defensible patches, individual females commonly defend particular patches and females are solitary while reductions in resource competition allow the formation of female groups (Jarman 1974, Clutton-Brock & Harvey 1978c, Clutton-Brock 2009b). Reproductive competition, too, can prevent the formation of female groups or limit their size. In some singular breeders, dominant females will tolerate the presence of young born the previous year but not of older individuals; in others, they will tolerate the presence of young that have not yet reached adult size; and, in a few they will tolerate the presence of offspring of all ages (Clutton-Brock & Lukas 2011). These differences are closely associated with contrasts in group size, which is typically smallest where dominant females will only tolerate young born the previous year (as in jackals and foxes) and largest where they will tolerate the presence of mature offspring, as in naked mole-rats (Clutton-Brock 2009b).

The intensity of reproductive competition between females also likely affects the proximate factors that constrain the size of groups. In singular breeders where dominant females evict adolescent subordinates, as in meerkats, group size may be regulated by social mechanisms that affect female tolerance and may vary within relatively narrow limits. In contrast, in species where the development of subordinates can be controlled by the dominant female and offspring are tolerated whatever their age (as in naked mole-rats), group size may vary more widely as a result of spatial and temporal variation in food availability. For example, in naked mole-rats, groups sometimes consist of several hundred individuals (Brett 1991).

Reproductive competition may also exert an important influence on the dynamics of group size in plural breeders. Where reproductive competition is intense, increases in group size are often associated with increased rates of abortion, infanticide and eviction (or dispersal) which progressively restrict recruitment and constrain the upper limits of group size (Hoogland 1995b, Kappeler & Fichtel 2011). In contrast, where increasing group size has little effect on the intensity of breeding competition between group members, females may form large groups whose size is ultimately limited by the effects of competition for resources on fecundity and survival (Prins 1996, Moss & Lee 2011).

Mating systems and sexual selection in males

Differences in female group size resulting from variation in female competition affect the potential for polygyny which, in turn, influences the degree of reproductive skew among males, the intensity of mating competition and the strength of sexual selection for traits that increase competitive success in males such as body size and weapon development (Clutton-BrockHarvey & Rudder 1977c, LindenforsGittleman & Jones 2007, Clutton-Brock & Albon 1989, Clutton-Brock 2009b). An additional consequence of contrasts in female group size is that it influences the frequency of competitive interactions between males and affects the tenure and longevity of resident males (Clutton-Brock & Isvaran 2007) with important consequences for average relatedness between group members and the genetic structure of populations (Clutton-Brock 2009b).

Reproductive skew in females

The intensity of female competition for breeding opportunities also affects the degree of reproductive skew among females. The highest levels of reproductive skew in female mammals are found in singular cooperative breeders where dominant females suppress the fertility of subordinate females (Clutton-Brock et al. 2006) (Clutton-Brock 2009c, Clutton-Brock 2009b). In these species, females can produce large litters at frequent intervals because their young are protected and fed by other group members, and variance in breeding success is often larger in females than in males (Hauber & Lacey 2005, Clutton-Brock *et al*. 2006). For example, in wild meerkats, the majority of females fail to breed while successful breeders can rear more than 80 offspring (Clutton-Brock 2009b). Reproductive success in both sexes is closely related to whether or not individuals acquire breeding roles and their length of tenure in breeding groups and as tenure is shorter in males than in females, standardized variance in lifetime breeding success is higher in females than males (Clutton-Brock et al. 2006).

Reproductive skew can also be high in plural breeders where the rank of females affects their breeding success and the survival of their offspring, like spotted hyenas (Holekamp and Szykman 1996) and savannah baboons (Silk et al. 2009, Pusey 2012) but it is unlikely to approach levels observed in singular cooperative breeders. However, in some of these species, the rank and breeding success of females depends on assistance from their relatives (see before) so that high rank may generate indirect benefits and measures of reproductive skew based on direct fitness only may underestimate the potential strength of selection operating on traits that improve the competitive success of females.

While reproductive skew among females can reach higher levels in singular cooperative breeders, like meerkats and mole-rats, the frequency of overt contest between females is often higher in plural than singular breeders. However, following the death of a dominant female in singular breeders, all adult females commonly fight for her position, their contest can be lethal (Reeve & Sherman 1991, Clutton-Brock et al. 2006) and selection on traits affecting success in these contests is likely to be very strong (Clutton-Brock et al. 2006). This illustrates the important point that there is not necessarily a close relationship between the frequency of competitive interactions or overt aggression and either the degree of reproductive skew or the intensity of selection on traits influencing success in competitive encounters.

Supportive relationships between females

Reproductive competition between breeding females may also be responsible for the evolution of supportive relationships that help females to establish and maintain their rank and that of their matriline (Silk 2007b, CheneySilk & Seyfarth

2012). Across species, the occurrence of regular supportive relationships and dependant rank system is associated with the formation of relatively large, stable groups including multiple breeding females where some females are close relatives while others are not, as in savannah baboons and spotted hyenas. The effects of social support on female dominance and fitness may, in turn, have led to the development of complex affiliative relationships that serve to maintain regular support (Clutton-Brock 2009a) as well as to tactics that minimise the tendency for social support to destabilise social relationships between competitors, including reassurance, reconciliatory behaviour and various forms of intervention (Aureli & van Schaik 1991, Aureli & de Waal 2000).

Female armaments

While traits that increase success in fights are rarely as highly developed in females as in males, intense competition between females for resources or breeding opportunities is sometimes associated with the development of traits enhancing competitive success. For example, in monogamous primates, where females compete for access to territories, the size of their canine teeth relatively to their body size is larger than in species where females are social and rely on support from other group members to defend their territories or ranges (HarveyKavanagh & Clutton-Brock 1978b, Plavcanvan Schaik & Kappeler 1995). Similarly, competition for resources may favour the evolution of female antlers and horns in some ungulates, although comparative studies suggest that female horns commonly represent an anti-predatory adaptation (Packer 1983, Stankowich & Caro 2009). For example, in reindeer and caribou, where females compete with each other (as well as with males) for craters in the snow to get access to food during the winter months, females carry antlers, in contrast to all other contemporary cervids, and females with larger antlers are more successful in obtaining access to limited food (Barrette & Vandal 1986). In Soay sheep, where some females are horned while others are hornless ('polled'), horned females are more likely to initiate and win aggressive interactions than polled ones (Robinson & Kruuk 2007) while studies of cattle show that the experimental removal of horns leads to reductions in the ability of individuals to dominate competitors in newly established groups (Boussou 1972). Comparative studies show that the distribution of female horns and antlers in ruminants is associated with variation in female group size (Roberts 1996) although other factors such as the need for effective defence against predators may also be involved (Packer 1983).

In some mammals, where female competition is unusually intense, females often show physiological, morphological and behavioural adaptations that increase their competitive abilities (Clutton-Brock et al. 2006) as they do in a wide range of other animals (West-Eberhard 1983, West-Eberhard 1984, TobiasMontgomerie & Lyon 2012). For example, in spotted hyenas, where females compete intensely to raise offspring, well-defined female hierarchies are associated with high levels of reproductive skew and dominant females show elevated testosterone levels, large body size and social dominance over males (GoymannEast & Hofer 2001, East & Hofer 2002, Holekamp & Dloniak 2009, East & Hofer 2010). Many of the same traits are found in social lemurs and are thought to be associated with intense competition between breeding females for resources in a fluctuating and unpredictable environment (Jolly 1984, Wright 1999, Dunham 2008). As would be expected as a result of high levels of reproductive skew, traits likely to affect competitive ability are also unusually well developed in females of some singular cooperative breeders. For example, in meerkats and naked mole-rats, females that acquire the breeding position show increased levels of circulating testosterone (Faulkes & Abbott 1997, Clutton-Brock et al. 2006) as well as a period of secondary growth that is reduced or absent in males and may help them to maintain their status and reproductive output (O'Riain & Braude 2001, Russell *et al.* 2004, Clutton-Brock *et al*. 2006). Breeding females are commonly the largest individuals in their group and are socially dominant to all group members (Reeve & Sherman 1991, Faulkes & Abbott 1997, Clutton-Brock et al. 1998b, Clutton-Brock et al. 2001b).

Females of domestic cattle provide additional evidence that selection in female competitiveness can lead to increased levels of aggression in females and enhanced testosterone levels. In some parts of Switzerland, domestic cattle are forced to fight with each other in tournaments before they are moved up in the summer pastures and their owners bet on their performance. Breeds used in these tournaments have been subject to some selection for fighting for a considerable period, show enhanced testosterone levels and are usually dominant to females of other breeds where females have not been selected for the same purpose (Plusquellec & Boussou 2001).

Female masculinisation and sexual mimicry

In several plural breeders where female competition is unusually intense, the genitalia of mature females show signs of masculinisation which in some cases, appear to mimic male traits (Licht *et al.* 1992, Licht *et al.* 1998, Glickman *et al.* 1998, Drea *et al.* 1998). For example, in spotted hyenas, mature females have an extended clitoris that mimics the male's penis and the sexes can be difficult to tell apart (Kruuk 1972, Glickman *et al*. 1998). Although hyenas are the best known example, the genitalia of adult females also show evidence of masculinisation in other species where females compete intensely, including some lemurs and golden moles (OstnerHeistermann & Kappeler 2003, Drea 2007).

Early explanations of masculinisation of female genitalia suggested that it represented a non-adaptive by-product of elevated maternal androgen levels affecting sexual differentiation during early development, or of increased sensitivity to androgens (Racey & Skinner 1979, Frank 1997). However, several empirical observations suggest that this is not an adequate explanation. First, experimental suppression of androgenisation during pregnancy does not prevent female genital masculinisation, suggesting that genetic factors are involved (Drea *et al*. 1998). Second, genital masculinisation can disappear when individuals reach an age where it no longer serves any purpose. For example, transient masculinisation has recently been found in two solitary carnivores, the Malagasy fossa (Hawkins *et al.* 2002) and the striped hyena (Wagner *et al.* 2007) as well as in redfronted lemurs (BartholdFichtel & Kappeler 2009). In fossas, juvenile females develop an enlarged spinescent clitoris supported by an os clitoridis and a pigmented secretion on the fur under-parts which, in adults, is confined to males (Hawkins *et al*. 2002). In addition, in the sexually dichromatic red-fronted lemurs, where competition among females is intense, female infants show transient "fur masculinisation" (BartholdFichtel & Kappeler 2009).

One possible explanation is that sexual mimicry may allow young females to deflect aggression from other females. For example, in spotted hyenas, it has been proposed that the striking pseudo-penis and pseudo-scrotum of female spotted hyenas may allow females to reduce the aggression they receive from strangers when crossing the territory of another group (Muller & Wrangham 2002). However, other explanations have been suggested (East *et al.* 2003). Adaptive explanations of sexual mimicry are strengthened by evidence that, in some species where there is intense competition between males, adolescent males show evidence of transient feminisation. For example, in red colobus monkeys, adolescent males show a transient development of the perineal area that resembles the extended clitoris of receptive females (Kuhn 1972).

Female ornamentation

As in males, reproductive competition between females has also led to the evolution of ornaments that signal their condition and reproductive status to the opposite sex. For example, female facial colouration in several cercopithecine monkeys is brighter during the fertile phase of their oestrus cycles than at other times (Dubuc *et al.* 2009, SetchellWickings & Knapp 2006). Similarly, the detailed structure of copulatory calls given by females changes with their stage of oestrus (O'Connell & Cowlishaw 1994, Semple *et al.* 2002) and playback experiments show that males discriminate between calls given by females at different stages of their cycle and are most attracted to the calls of females in late oestrus (Semple & McComb 2000).

One of the most striking examples of female ornaments are the cyclical perineal swellings found in monkeys and apes that live in multi-male groups where males have access to multiple partners (Clutton-Brock & Harvey 1976, Zinner *et al.* 2004). In these species, females can gain support and protection for themselves and their offspring from males they consort with and may increase their direct fitness by attracting and mating with multiple males (Smuts 1985, Palombit 2000, Alberts & Fitzpatrick 2012). The long duration of perineal swellings relatively to the fertile (periovulatory) period may allow females to mate with multiple males when the probability of ovulation is not maximal, which may help to confuse paternity certainty and decrease infanticide risk for future offspring (Nunn 1999). Males may maximise their direct fitness by mating with females with large swellings for the size and colouring of female sexual swellings varies throughout the menstrual cycle of females, providing an approximate indicator of variation in fecundity (Zinner et al. 2004, Plavcan 2004, Emery & Whitten 2003, Higham *et al.* 2008, Higham *et al.* 2009). Consequently, the gradual nature of the signal may allow females to concentrate paternity in a high-ranking male at times where ovulation probability is maximal to secure paternal care for their future offspring (Nunn 1999, Alberts & Fitzpatrick 2012). Moreover, in several species, individual differences in the relative size of the swellings (which are consistent across cycles) are positively correlated with the female's body condition and reproductive success (Domb & Pagel 2001, Huchard *et al.* 2009). As might be expected, large swellings are more effective in attracting males and evolutionary models suggest that swellings may have originated as a signal of receptivity and subsequently evolved to signal differences in individual quality (Huchard et al. 2009).

The evolution of traits that enhance female competitiveness raises questions about the mechanisms limiting their development. In males, the evolution of traits that enhance competitive ability is often associated with reductions in their survival as juveniles, adolescents and adults (Clutton-BrockAlbon & Guinness 1985). However, there is little evidence of a similar reduction in female survival in species where reproductive competition is intense and secondary sexual characters are highly developed in females (Clutton-Brock 2009c). One possibility is that the costs of expenditure by females on competition or ornamentation depress fecundity before they reach a level at which they have measurable costs to female survival, and that costs to fecundity constrain the development of secondary sexual characters (FitzpatrickBerglund & Rosenqvist 1995, LeBas 2006). For example, elevated levels of testosterone may have adverse effects on the fecundity of females or on the development of their offspring which constrain the evolution of further increases in female competitiveness (Packer et al. 1995, Drea *et al.* 2002, Knickmeyer & Baron-Cohen 2006). However, as yet, few studies have explained the magnitude and distribution of these effects.

Summary

In summary, competition for resources and breeding opportunities is widespread in female mammals and the success of individuals in competitive encounters affects all components of their fitness. In some species, both the extent of reproductive skew and the intensity of selection on traits that enhance competitive success are greater in females than in males. However, overt fighting between females is seldom as common as among males and the development of sexually selected weaponry in females is rarely as extreme as in males. Instead, females commonly use social strategies to enhance their reproductive success, which may explain why females are commonly more responsive than males to social signals and relationships (Mealey 2000).

Despite the presence of these differences, the underlying mechanisms affecting fitness in the two sexes are fundamentally similar. As in males, females commonly compete to maintain exclusive access to resources and mates as well as to attract members of the opposite sex. In recent years, the underlying similarity in the operation of selection in males and females has sparked a debate over whether or not reproductive competition between females should be regarded as a form of sexual selection or whether it should be allocated to some other category of selection, such as social selection (West-Eberhard 1983, West-Eberhard 1984, Carranza 2010, Shuker 2010, Stockley & Bro-Jorgensen 2011, Clutton-Brock 2009c, Clutton-Brock 2010, Lyon & Montgomerie 2012, Tobias, Montgomerie & Lyon 2012). Whichever approach is adopted, the existence of this discussion underlines the qualitative similarity in the evolutionary mechanisms operating in both sexes.

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