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Female competition and its evolutionary consequences in mammals

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ABSTRACT

Following Darwin's original insights regarding sexual selection, studies of intrasexual competition have mainly focused on male competition for mates; by contrast, female reproductive competition has received less attention. Here, we review evidence that female mammals compete for both resources and mates in order to secure reproductive benefits. We describe how females compete for resources such as food, nest sites, and protection by means of dominance relationships, territoriality and inter-group aggression, and by inhibiting the reproduction of other females. We also describe evidence that female mammals compete for mates and consider the ultimate causes of such behaviour, including competition for access to resources provided by mates, sperm limitation and prevention of future resource competition. Our review reveals female competition to be a potentially widespread and significant evolutionary selection pressure among mammals, particularly competition for resources among social species for which most evidence is currently available.

We report that female competition is associated with many diverse adaptations, from overtly aggressive behaviour, weaponry, and conspicuous sexual signals to subtle and often complex social behaviour involving olfactory signalling, alliance formation, altruism and spite, and even cases where individuals appear to inhibit their own reproduction. Overall, despite some obvious parallels with male phenotypic traits favoured under sexual selection, it appears that fundamental differences in the reproductive strategies of the sexes (ultimately related to parental investment) commonly lead to contrasting competitive goals and adaptations. Because female adaptations for intrasexual competition are often less conspicuous than those of males, they are generally more challenging to study. In particular, since females often employ competitive strategies that directly influence not only the number but also the quality (survival and reproductive success) of their own offspring, as well as the relative reproductive success of others, a multigenerational view ideally is required to quantify the full extent of variation in female fitness resulting from intrasexual competition. Nonetheless, current evidence indicates that the reproductive success of female mammals can also be highly variable over shorter time scales, with significant reproductive skew related to competitive ability.

Whether we choose to describe the outcome of female reproductive competition (competition for mates, for mates controlling resources, or for resources *per se*) as sexual selection depends on how sexual selection is defined. Considering sexual selection strictly as resulting from differential mating or fertilisation success, the role of female competition for the sperm of preferred (or competitively successful) males appears particularly worthy of more detailed investigation. Broader definitions of sexual selection have recently been proposed to encompass the impact on reproduction of competition for resources other than mates. Although the merits of such definitions are a matter of ongoing debate, our review highlights that understanding the evolutionary causes and consequences of female reproductive competition indeed requires a broader perspective than has traditionally been assumed. We conclude that future research in this field offers much exciting potential to address new and fundamentally important questions relating to social and mating-system evolution.

Key words: sexual selection, female competition, sperm limitation, sexual conflict, reproductive suppression, sexual signalling, infanticide, cooperation, spite, sex-dependent selection.

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I. INTRODUCTION

Darwin (1871) regarded sexual selection as depending on "the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction" (p256). Subsequent research efforts in the field have focused mainly on understanding the causes and consequences of competition for mates, with emphasis on intrasexual selection due to male mate competition and intersexual selection generated by female mate choice—both originally identified by Darwin (1871) as the most important causes of sexual selection (Andersson, 1994; Clutton-Brock, 2004). More modern theory explains these general patterns as resulting from sex differences in the costs of producing gametes and rearing offspring, which are typically greater for females (Bateman, 1948; Trivers, 1972). Because males usually have higher potential reproductive rates than females, it can be argued that males have more to gain from being competitive (Clutton-Brock & Vincent, 1991; Clutton-Brock & Parker, 1992). Indeed, variance in reproductive success often appears to be greater among males, and sexual selection is expected to be stronger in this sex as a consequence (Bateman, 1948; Payne, 1979; but see Sutherland, 1985; Grafen, 1988).

Recent developments in the field of sexual selection can be attributed in part to more detailed exploration of female influences beyond mate choice. In particular, it is now recognised that females of diverse animal taxa typically mate with more than one male per reproductive event (Jennions & Petrie, 2000; Hosken & Stockley, 2003). Sexual selection can thus extend beyond copulation, with potentially far-reaching consequences for the evolution of both male and female reproductive strategies (Parker, 1970; Eberhard, 1996; Zeh & Zeh, 2003). Increasing emphasis on interactions between the sexes has also generated growing awareness of the importance of sexual conflict (Parker, 1979), both as a powerful selective force and a potential constraint in the evolution of secondary sexual traits (Arnqvist & Rowe, 2005; Tregenza, Wedell & Chapman, 2006). Importantly, research into sexual conflicts has emphasised that genes which have a selective advantage when expressed in one sex may be selected against when expressed in the other (Foerster *et al.*, 2007; Carranza *et al.*, 2009), which underlines the importance of taking a multi-generational view when attempting to quantify variation in reproductive success and the strength of sexual selection (Hunt *et al.*, 2004).

In addition to these developments, a shift in emphasis to a broad definition of sexual selection based on competition in the context of reproduction, rather than for access to mates *per se*, has recently been proposed, in order to encompass largely neglected aspects of female competition for resources other than mates. It is argued that the effect of intrasexual selection due to variance in resource acquisition, particularly in females, has been overlooked and may have led to the strength of sexual selection on females being underestimated relative to males (Clutton-Brock *et al.*, 2006; Clutton-Brock, 2007, 2009). A broader definition still is proposed by Carranza (2009), who calls for sexual selection to be regarded as 'those natural selection forces that operate differently in males and females because of the strategies of the sexes' (p 750).

Our aim in the present review is to investigate the nature and consequences of competition among female mammals, and to consider the potential role of female competition in sexual selection according to various definitions. Mammals provide many conspicuous examples of traditional sex roles linked to sexual selection, from the dramatic male weaponry and combat that inspired Darwin's 'law of battle', to the costly female strategy of lactation that, as an extreme form of parental investment, offers an appealing explanation for intense sexual selection on males. Nonetheless, the group has also generated several recent studies with significant potential to broaden traditional perspectives on sexual selection and reproductive competition (Clutton-Brock *et al.*, 2006; Bro-Jørgensen, 2007*a*; Foerster *et al.*, 2007; Emery Thompson *et al.*, 2007). We begin by reviewing literature on competition between females for resources needed for reproduction, providing evidence of numerous diverse and often cryptic competitive strategies that may commonly result in significant reproductive skew. Next we review evidence of female competition for mates and consider potential causes of such competition. Based on the patterns emerging, we subsequently assess the implications of our review for understanding how sexual and natural selection influence female competitive strategies in the context of reproduction. We conclude by discussing how different aspects of intrasexual competition between both males and females can be encompassed within a broad conceptual framework.

II. FEMALE COMPETITION FOR RESOURCES

Competition between female mammals for resources other than mates can have important reproductive consequences. In particular, high energetic demands of lactation and gestation (Loudon & Racey, 1987; Gittleman & Thompson, 1988) mean that the reproductive success of female mammals is often likely to be constrained by access to food (e.g. Emlen & Oring, 1977; Wrangham, 1980; Ims, 1987; Sterck, Watts & van Schaik, 1997). As described below, other potentially limiting resources for which females compete include shelter (e.g. nest sites, favourable positions to avoid predation) and assistance with offspring care and protection.

(1) Dominance and priority of access to resources

In group-living or gregarious species where individuals regularly associate with one another (or in solitary species with regular interaction between familiar individuals), females often establish dominant-subordinate relationships (Rowell, 1974; Kaufmann, 1983). Dominant females may achieve access to more or better quality food than subordinates, feed more efficiently (i.e. expend less energy or time in obtaining food), supplant others from favoured feeding sites more often, and/or receive fewer interruptions when feeding (e.g. Whitten, 1983; Barrette & Vandal, 1986; Harcourt, 1987; van Noordwijk & van Schaik, 1987; Barton, 1993; Barton & Whiten, 1993; Vogel, 2005). For example, high-ranking female chimpanzees (*Pan troglodytes*) forage more efficiently and have higher diet quality that subordinate females (Murray, Eberly & Pusey, 2006), and dominant bison cows (*Bison bison*) have higher foraging efficiency than subordinates during snow cover periods (Rutberg, 1986). Differences in food quality and/or foraging efficiency can have important consequences for female condition. During periods of intense competition in the winter, high-ranked female reindeer (*Rangifer tarandus*) have access to better foraging areas and gain body mass whereas low ranked females instead lose body mass (Espmark, 1964; Holand *et al.*, 2004*b*).

In addition to gaining improved access to food, dominant females can also gain priority of access to other resources that are essential to their survival and/or reproductive success. For example, during a period of water shortage, higher ranking female vervet monkeys (*Cercopithecus aethiops*) had access to preferred drinking sites (Wrangham, 1981). Access to food and water is less likely to be limiting for commensal species such as house mice (*Mus musculus domesticus*), but in high-density populations, some females are apparently unable to reproduce as a consequence of restricted access to nest sites (Hurst, 1987).

Dominant females may also gain fitness advantages by minimising the risk of predation. Among long-tailed macaques (*Macaca fascicularis*), high-ranking females are more likely to gain a central position in 'safe' main foraging parties (van Noordwijk & van Schaik, 1987). Moreover, the mortality of female chacma baboons (*Papio cynocephalus ursinus)* in a population subject to high predation risk was significantly related to dominance rank, leading Ron, Henzi & Motro (1996) to suggest that higher ranking females may be better protected from predation through access to more central spatial positions in the troop.

Does priority of access to resources translate into reproductive benefits? Where evidence exists that dominant females gain priority of access to limited resources, it is usually assumed that this will translate into improved reproductive success. However, evidence of a direct link between the quality or quantity of resources obtained by females and their reproductive success under natural conditions is still relatively scarce. Some of the best evidence that improved reproductive success is linked to priority of access to favoured foraging areas comes from long-term studies of female chimpanzees (Pusey, Williams & Goodall, 1997; Emery Thompson *et al.*, 2007; Kahlenberg, Emery Thompson & Wrangham, 2008). Although direct aggression over food is rare, there is wide variation in fitness among females that has been linked to social status (Pusey *et al.*, 1997). Emery Thompson *et al.* (2007) found that differences in reproductive success may be at least partly explained by the quality of food that females can regularly access; those that are able to forage in areas containing more preferred foods have elevated ovarian hormone production, shorter interbirth intervals and higher infant survivorship. Similarly, long-term studies of spotted hyenas (*Crocuta crocuta*) have revealed differences in reproductive success that apparently result from competition for food. While the reproductive success of high-ranking females is consistently greater than that of low-ranking females and does not vary with prey abundance, the reproductive success of low-ranking females is significantly improved when prey animals are abundant (Holekamp, Smale & Szykman, 1996). Further examples where improved reproductive success of high-ranking females may be explained by priority of access to resources (although typically based on less direct evidence) are summarised in Table 1.

It is important to emphasise that while improved reproductive success among dominant females appears to be widespread in a variety of mammal species (Table 1), not all studies have found evidence of such effects (e.g. Wolfe, 1984; Eccles & Shackleton, 1986; Harcourt, 1987; Meikle & Vessey, 1988; Ellis, 1995). In some cases, this may be because resources were not a limiting factor during the sampling period. For example, Gouzoules, Gouzoules & Fedigan (1982) found no effect of social dominance on the reproductive success of female Japanese macacques (*Macaca fuscata*) in a provisioned population over eight years. Studies of managed or provisioned populations may typically be less informative, although some have revealed significant effects (e.g. Meikle & Vessey, 1988; Paul, Kuester, & Arnemann, 1992; Cassinello & Alados, 1996; Vervaecke, Roden & De Vries, 2005; Pluháček, Bartoš & Čulík, 2006). Similarly, fluctuations in resource availability in natural populations could mean that long-term studies are more likely to reveal reproductive benefits associated with social status. This is partly because differences in reproductive success according to social status may only be detectable under conditions of moderate to severe resource limitation (e.g. Woodroffe & Macdonald, 1995), but also because such differences may occasionally be overridden if conditions of resource limitation become extreme. During a long-term study of yellow baboons (*Papio cynocephalus*), the majority of rank effects on measures of lifetime reproductive success were virtually eliminated for mothers reproducing during a population decline (Wasser *et al.*, 2004). As the population crashed, so did the variance in female lifetime reproductive success within social groups. These findings indicate that the impact of social status on female reproductive success can be drastically altered by extrinsically mediated demographic events. Demographic factors may also obscure effects of rank on female reproductive success when considering patterns across the population as a whole (see also Beehner *et al.*, 2006). In ring-tailed lemurs (*Lemur catta*), low-ranking females have fewer surviving infants only in relatively large groups (Takahata *et al.*, 2008), and in mountain goats (*Oreamnos americanus*) the effects of rank on kid production appear to be more pronounced for young females (Côté & Festa-Bianchet, 2001).

(2) Territoriality and inter-group aggression

Territorial aggression often occurs in association with the active defence of a home range by an individual or group, and is aimed at the repulsion of potential intruders. The main function of territorial aggression is typically to maintain exclusive access to some limiting resource, such as food, shelter or space (e.g. Boonstra & Rodd, 1983; Ostfeld, 1985; Gray, Jensen & Hurst, 2002). For example, in species such as microtine rodents that have relatively low-quality diets, there is evidence that food may often be a limiting resource for females during the reproductive season, and that female territorial behaviour is most pronounced when food is sparse, patchy and slowly renewable, and when population density is low to moderate (Ostfeld, 1985–see also Ims, 1987; Ostfeld, 1990). In such species, the ability to defend a territory may have an important role in determining the amount of resources available for reproduction, and hence current reproductive success (e.g. Koskela, Mappes & Ylönen, 1997), although additional benefits of territory defence, such as long-term resource availability for offspring (Boonstra & Rodd, 1983) or infanticide avoidance (Wolff, 1993; Fortier & Tamarin, 1998), are also possible. Territorial aggression directed at same-sex conspecifics in communally breeding species has also been linked to the defence of non-reproductive helpers, as an additional 'resource' contributing to female reproductive success. In experimental studies of captive golden lion tamarins (*Leontopithecus rosalia*), resident females direct high levels of attack and agonistic displays towards female intruders, and females in groups with more helpers present exhibit higher levels of aggression (French & Inglett, 1989).

For group-living species, intergroup resource competition can be a significant source of escalated aggression, and females may cooperate in competing with rival groups. Indeed, Wrangham (1980) proposed that cooperation among female kin is the main reason for primates living together in female-bonded groups (see also Sterck *et al.*, 1997), and some support for this hypothesis has also been reported for other taxa (e.g. spotted hyenas: Frank, 1986). Lions (*Panthera leo*) provide an interesting example of intergroup competition because females within groups are generally quite egalitarian (Packer, Pusey & Eberly, 2001). However, intergroup competition is a major determinant of reproductive success; females vigorously defend territories against neighbouring prides, and attacks can be fatal (Packer *et al.*, 1988; Packer, Scheel & Pusey, 1990; Mosser & Packer, 2009). Similarly, while serious fighting between female spotted hyenas is apparently rare within clans, fights between neighbouring clans are generally more intense (Frank, 1986). Inter-group competition between female ring-tailed lemurs increases substantially during the birth season and can result in loss of infants (Erhart & Overdorff, 2008). Where individual reproductive success depends on the relative size of competing groups, it has also been suggested that females might compete to attract more males to their group (Wrangham, 1980).

In some cases, social groups have been observed to take control of resources previously controlled by a rival group.

Table 1. Examples of various components of reproductive fitness linked to social dominance in female mammals. In each case, higher reproductive success or survival of dominant females may at least partly be explained by differential access to more and/or better quality resources

Component of reproductive fitness higher for dominant females	Examples	Evidence	Source
Early onset of oestrus/pregnancy	Red deer *Cervus elaphus*	Dominant hinds conceive and calve on average five days earlier than subordinates.	Clutton-Brock *et al.* (1986)
	Reindeer *Rangifer tarandus*	Date of birth is earlier for high-ranked females than subordinates.	Holand *et al.* (2004*b*)
	Yellow baboon *Papio cynocephalus*	High-ranking females reach menarche earlier.	Bercovitch & Strum (1993); Wasser *et al.* (2004)
More offspring per litter	Meerkats *Suricata suricatta*	Dominant females increase in body size and large females deliver larger litters.	Russell *et al.* (2004)
Higher rate of reproduction	Red deer *Cervus elaphus*	Dominant hinds show a tendency to calve more often.	Clutton-Brock *et al.* (1986)
	Reindeer *Rangifer tarandus*	Fecundity is positively related to female rank.	Holand *et al.* (2004*b*)
	Barbary sheep *Ammotragus lervia*	Maternal social rank is positively related to number of lambs produced.	Cassinello & Alados (1996)
	Mountain goat *Oreamnos americanus*	Females dominant for their age have a higher probability of producing a kid.	Côté & Festa-Bianchet (2001)
	Yellow baboon *Papio cynocephalus*	High-ranking females have more offspring and shorter inter-birth intervals.	Altmann & Alberts (2003); Wasser *et al.* (2004)
	Long-tailed macaque *Macaca fascicularis*	High-ranking females are more likely to give birth again when they had a surviving offspring the year before.	van Nordwijk & van Schaik (1999)
	Chimpanzee *Pan troglodytes*	High-ranking females produce offspring at a significantly more rapid rate; shorter inter-birth intervals linked to density of preferred food resources in core foraging areas.	Pusey *et al.* (1997); Emery Thompson *et al.* (2007)
	Spotted hyena *Crocuta crocuta*	Dominant females have better access to resources and shorter inter-birth intervals.	Frank 1986; Holekamp *et al.* (1996)
	Red squirrel *Sciurus vulgaris*	Dominant females are heavier and have a higher probability of being fertile than subordinates.	Wauters & Dhont (1989)
Larger offspring/faster growth rate	Red deer *Cervus elaphus*	Dominant hinds produce heavier calves than subordinates.	Clutton-Brock *et al.* (1986)
	Reindeer *Rangifer tarandus*	Early pre-weaning growth rate and body mass of calves increase with female social rank.	Holand *et al.* (2004*b*)
	Bison *Bison bison*	Offspring weaning mass correlates with maternal rank.	Vervaecke *et al.* (2005)
	Southern elephant seal *Mirounga leonina*	High-status cows rear larger pups.	McCann (1982)
	Spotted hyena *Crocuta crocuta*	Offspring of high-ranking females grow faster.	Hofer & East (2003)

Table 1. *(Cont.)*

Component of reproductive fitness higher for dominant females	Examples	Evidence	Source
Higher offspring survival	Red deer *Cervus elaphus*	Calves of dominant hinds have a higher probability of surviving to maturity.	Clutton-Brock *et al.* (1986)
	Rhesus macaque *Macaca mulatta*	Sons of high-ranking females have higher survivorship.	Meikle & Vessey (1988)
	Northern elephant seal *Mirounga angustirostris*	Older females have higher social dominance and a higher probability of weaning healthy pups.	Reiter *et al.* (1981) van Nordwijk & van Schaik (1999)
	Long-tailed macaque *Macaca fascicularis*	Survival of infants (not juveniles) is rank dependent.	
	Chimpanzee *Pan troglodytes*	High-ranking females have significantly higher infant survival; higher infant survivorship linked to density of preferred food resources in core foraging areas.	Pusey *et al.* (1997); Emery Thompson *et al.* (2007)
	Spotted hyena *Crocuta crocuta*	Offspring of high-ranking females have a better chance of survival to adulthood.	Hofer & East (2003)
Higher offspring reproductive success	Barbary macaque *Macaca sylvanus*	Sons of high-ranking females begin to reproduce significantly earlier and sire significantly more infants surviving to at least one year of age during the first four years of their reproductive career compared to sons of low ranking females.	Paul *et al.* (1992)
	Long-tailed macaque *Macaca fascicularis*	Sons of high-ranking females are more likely to become top dominant in another group.	van Nordwijk & van Schaik (1999) Pusey *et al.* (1997)
	Chimpanzee *Pan troglodytes*	High-ranking females have significantly faster maturing daughters.	
	Spotted hyena *Crocuta crocuta*	Daughters of high-ranking females give birth to their first litter at an earlier age than daughters of low-ranking mothers.	Hofer & East (2003)
Increased longevity	Vervet monkey *Cercopithecus aethiops*	Mortality of females is rank-related because of survival through critical periods of resource limitation–e.g. during severe drought.	Wrangham (1981)
	Long-tailed macaque *Macaca fascicularis*	High-ranking females are more likely to gain a central position in 'safe' main foraging parties, and mortality is greater for females outside of the main parties. High-ranking females have longer reproductive careers.	van Nordwijk & van Schaik (1987) van Nordwijk & van Schaik (1999)

For example, Dittus (1986) observed the consequences when a group of toque macaques (*Macaca sinica*) took over the home-range of one of its subordinate neighbourhood groups. In the seven years before the take-over, the dominant group had consistently won all contests at common feeding sites, but the reproductive success of the females in the two groups was not significantly different. After the take-over, the females of the subjugated group occupied the lowest ranks of the merged group, and their survivorship and reproductive success was significantly lower than among females of the dominant subgroup. Indirect evidence of territorial take-overs by female groups has also been reported for European badgers, *Meles meles* (Woodroffe, Macdonald & Da Silva, 1995). Females dispersed from their home territory in coalitions of two or three, over relatively long distances, to territories occupied by single females. The single resident females disappeared following the arrival of the immigrants, suggesting that territory take-overs had occurred.

Aggression may also occur between competing matrilines where females associate within larger social groups. Here, co-ordinated aggression may even result in eviction of competitors from the group, as has been reported for lemurs under both captive and natural conditions (Vick & Pereira, 1989; Digby, 1999; Pochron, Tucker & Wright, 2004; Ichino, 2006). In ring-tailed lemur groups, persistent aggression may be targeted at one or two individuals over a protracted period until they leave the group. Where groups consist of different families, coalitions are likely to be formed between related females, with aggression directed at unrelated females in conjunction with oestrous cycling or births (Vick & Pereira, 1989; Ichino, 2006). Resource competition is implicated as the ultimate cause of such aggression, since it is most often observed after groups have reached critical sizes (Vick & Pereira, 1989).

(3) Inhibiting the reproduction of others

Competitive strategies aiming at inhibiting the reproduction of others are commonly observed among female mammals living in relatively stable social groups. Resource competition may often explain such behaviour, under the assumption that fewer competitors means that more resources will be available for successfully reproducing females and their kin (Wasser & Barash, 1983).

From the perspective of competitively superior females, suppressing the reproduction of others may often be an adaptive competitive strategy. Benefits include increased resources that can be used to increase the number and/or quality of offspring produced, and can also include help with rearing offspring (including care and in some cases milk), for example by monopolising available helpers or by coercing the females that are being suppressed to invest in the suppressor's offspring. Alternatively or additionally, suppression of others may function in the longer term to ensure sufficient resources are available for the descendants of reproducing females (see also Section III.3). Hence from a broader perspective, suppression of competitors' reproduction may be viewed as a form of lineage competition, success in which increases representation of a female's descendants in subsequent generations under conditions where both reproduction and survival are ultimately constrained by resource limitation.

The way in which suppression is imposed at a proximate level can be direct, *via* interference, harassment or aggression (e.g. Dunbar & Dunbar, 1977; Hrdy, 1979; Silk *et al.*, 1981; Rhine, Wasser & Norton, 1988; Wasser & Starling, 1988; Clutton-Brock *et al.*, 1998; Hackländer, Möstl & Arnold, 2003), or indirect, *via* signals that communicate social dominance and can influence the reproductive and life-history decisions of young or subordinate females (e.g. Epple & Katz, 1984; Savage, Ziegler & Snowdon, 1988; Barrett, Abbott & George, 1993; Saltzman, Digby & Abbott, 2009). Such stimuli induce responses at different stages of the reproductive cycle from inhibition of mating (see Section III.3) to delayed sexual maturity, disruption of ovulation, implantation, or spontaneous abortion (e.g. Bowman, Dilley & Keverne, 1978; Huck, Bracken & Lisk, 1983, Huck *et al.*, 1988*b*; Adams, Kaplan & Koritnik, 1985; Harcourt, 1987, Creel *et al.*, 1992; Faulkes & Abbott, 1997; Solomon *et al.*, 2001; Hackländer *et al.*, 2003; Saltzman *et al.*, 2006, 2009). Prolonged stress associated with social harassment may also result in reduced lifespan, with further long-term consequences for reproductive success (von Holst *et al.*, 2002; Epel *et al.*, 2004; Sapolsky, 2005).

(*a*) *Reproductive suppression*

Aggression directed towards adult conspecific females may often function to inhibit their reproduction. Wasser & Barash (1983) noted that because reproduction is so costly for female mammals, they have evolved a variety of mechanisms that allow investment in rearing offspring to be postponed under unfavourable conditions (see also Bronson, 1989). When such mechanisms involve inhibition of reproduction under stress (e.g. Bowman *et al.*, 1978; Adams *et al.*, 1985), they can be triggered by persistent aggressive harassment by conspecific females (termed 'social suppression' by Wasser & Barash, 1983).

Some of the first evidence of social harassment among females in natural populations came from studies of gelada baboons, *Theropithecus gelada* (Dunbar & Dunbar, 1977; Dunbar, 1980). Dominant female geladas typically conceive before subordinates, and harass subordinate females in their units more when the subordinates are in oestrus. Since both dominant and subordinate females receive similar numbers of ejaculations, Dunbar & Dunbar (1977) hypothesised that harassment by dominant females might disrupt the ovulatory cycle of subordinates. Further evidence for persistent harassment of subordinates comes from a study of female coalition attacks among yellow baboons (Wasser & Starling, 1988). Such attacks are directed particularly towards cycling females in the follicular phase, resulting in an increased number of cycles to conception. Since the attackers often include pregnant or other non-sexually receptive females, competition for sperm again seems unlikely. Rather it appears that females attempt to suppress the reproduction of others at predictably competitive times when there is a high level of reproductive synchrony, and that by doing so they reduce the competition for their own offspring from the time they are weaned (Wasser & Starling, 1988). Similarly, dominant female Alpine marmots (*Marmota marmota*) make no attempt to prevent subordinates from mating but initiate significantly more agonistic interactions against subordinate females during the gestation period (Hackländer *et al.*, 2003). Subordinate females in this study subsequently did not produce litters, and reproductive suppression in this species is apparently mediated by negative effects of stress (measured as an increased level of glucocorticoids) on the activity of the hypothalamic-pituitary-gonadal axis. Suppression of reproduction in subordinate female meerkats (*Suricata suricatta*) has also been linked to a stress response induced by dominant females (Young *et al.*, 2006). In this case, when dominant females are pregnant, they subject selected subordinate females to escalated aggression, which results in temporary eviction from the group. Subordinate females suffer a chronic stress response in response to eviction, including elevated glucocorticoid adrenal hormone levels, leading to reduced conception rates and an increased rate of spontaneous abortion. Moreover, the females that are targeted for aggression by dominant females are their most likely competitors—older, pregnant and more distantly related females (Young *et al.*, 2006). Evidence of abortion induced by the stress of eviction has also been reported for banded mongooses (*Mungos mungo*) (Gilchrist, 2006). In this case evictions are relatively rare but appear more likely to occur in groups with relatively high numbers of reproductive females.

Although most examples of reproductive suppression come from group-living species, similar effects have also been reported for a solitary species, the golden hamster (*Mesocricetus auratus*), studied under both laboratory and semi-natural conditions (Huck *et al.*, 1988*a*,*b*). Brief interactions with socially dominant females lead to an increased incidence of implantation failure in socially subordinate females when interactions occur soon after mating, and increased fetal mortality when interactions occur during later pregnancy (Huck *et al.*, 1988*b*). Moreover, the extent of reproductive suppression recorded in subordinate females is correlated with the number of attacks and chases they experience (Huck *et al.*, 1988*a*).

In species with communal care of offspring, dominant females can gain substantial investment in their young by monopolising reproductive opportunities within their social group [a situation variously described as reproductive despotism or singular cooperative breeding (Solomon & French, 1997)]. Perhaps the most extreme example of singular cooperative breeding and associated extreme reproductive skew among females occurs in naked mole rats (*Heterocephalus glaber*), which live in large subterranean colonies and have a breeding system that may even be described as eusocial (Jarvis, 1981; Faulkes & Bennett, 2001). Breeding within a colony is typically monopolised by a single large dominant female, whose offspring are fed, groomed and protected by numerous closely related non-reproductive individuals (Jarvis, 1981; Reeve *et al.*, 1990; Lacey & Sherman, 1997; Faulkes & Abbott, 1997). The reproductive suppression of other females in the colony is apparently maintained by social contact with the breeding female, which involves frequent low-level aggressive interactions (Lacey & Sherman, 1997).

(*b*) *Infanticide and aggression towards competitors' offspring*

Aggression and harassment directed at the offspring of rival females can have significant fitness consequences for both mother and offspring. For example, Silk *et al.* (1981) report that the infants of captive low-ranking bonnet macaques (*Macaca radiata*) have a lower probability of surviving to six months of age than do the infants of other females, and their juvenile daughters are more vulnerable to behaviourally induced mortality. In both cases, this increased mortality risk results from aggression by unrelated, higher ranking females. The infants of low-ranking bonnet macaques are also more likely to be subject to attempted 'kidnapping' by unrelated females, which may be harmful to their survival (Silk 1980). Similarly, in natural populations, the offspring of low-ranking yellow baboons are more likely to experience 'rough handling' by unrelated females within their social group, and high levels of such handling are linked to increased infant mortality by age three months (Kleindorfer & Wasser, 2004). In Cape mountain zebra (*Equus zebra zebra*), Lloyd & Rasa (1989) found that dominant mares are aggressive towards subordinate mares' foals, and several cases of foal mortality were attributed to this aggression. Dominant mares also aggressively interrupt suckling bouts between subordinate mares and their foals by biting and chasing the mother, and this is likely to be particularly costly during drought periods when the foals of subordinate females may be more likely to die of starvation.

Numerous accounts exist of female mammals killing other females' offspring, among diverse mammalian taxa including rodents, carnivores, primates and lagomorphs (reviewed in Hrdy, 1979; Hausfater & Hrdy, 1984; Agrell, Wolff & Ylonen, 1998; Ebensperger, 1998). It is often assumed that female infanticide is related to resource competition, and there is circumstantial evidence for this in some cases. For example, female Belding's ground squirrels (*Spermophilus beldingi*) that lose infants by infanticide are more likely to leave their burrows, thereby making their abandoned nest sites available to infanticidal females (Sherman, 1981). Moreover, female infanticide is commonly reported in ground squirrels and other species for which a safe nest site is a critical resource for successful reproduction (Sherman, 1981, 1982; Balfour, 1983; Brody & Melcher, 1985; Trulio *et al.*, 1985), and infanticide is associated with territorial takeovers (Kunkele, 1992). Space (including both food and cover) is an important resource for which female small mammals compete (Ostfeld, 1985, 1990; Ims, 1987), and it has been suggested that female infanticide in such species may result from competition for space at high population density (Wolff & Cicirello, 1989). Assuming that some resource benefit results, theoretical models indicate that female infanticide can be an evolutionarily stable strategy, with the expectation that females will typically kill litters of nearby neighbours, thereby removing close competitors while keeping costs at a low level (Tuomi, Agrell & Mappes, 1997). Consumption of infant remains may also provide nutritional benefits (reviews in Hrdy, 1979; Ebensperger, 1998), although it can be difficult to ascertain if this is the primary function of killing (e.g. Wolff & Cicirello, 1989).

Investment in rearing offspring, either by the infanticidal female herself or by the mother of her victims, may also be considered as a resource for which females compete. In this context, infanticide can function to prevent exploitation of milk supplies by unrelated infants; female elephant seals (*Mirounga angustirostris*) attack and kill infants attempting to steal their milk (LeBoeuf & Briggs, 1977). In communal breeding systems, infanticide can also function to increase investment in care of the infanticidal female's own offspring by helpers. In the common marmoset (*Callithrix jacchus*), subordinate non-reproductive helpers contribute to the care of dominant females' offspring, and by killing any offspring produced by potential helpers, dominant females can increase the investment available for their own young (Digby, 1995; Lazaro-Perea *et al.*, 2000; Saltzman *et al.*, 2009). Only when the care of young produced by subordinate females does not overlap with lactation of the dominant female's own offspring are the subordinates' young likely to survive. Indirect evidence suggests that dominant female meerkats also frequently kill the offspring of subordinate females within their social group; an important predictor of whether a subordinate female's pups will survive to emergence is whether or not the dominant female is pregnant at the time of their birth (Clutton-Brock *et al.*, 1998, 2001).

In accordance with general expectations based on kin selection theory (Hamilton, 1964), infanticide is commonly directed at offspring of unrelated females rather than those of close relatives. For example, evidence from studies of Belding's ground squirrels (*Spermophilus beldingi*) suggests that infanticide is perpetrated by adult females that are distantly related to the offspring killed (Sherman, 1981), and experimental studies of bank voles (*Myodes glareolus*), demonstrate that familiarity between females decreases the frequency of infanticidal acts (Ylönen, Koskela & Mappes, 1997). Hrdy (1979) also notes that several well-documented examples of female infanticide occur in species where females move between communities, such as wild dogs (*Lycaon pictus*) and chimpanzees. Moreover, infanticide among female chimpanzees is reported under conditions of increased resource competition where immigrant females are competing with residents for limited foraging areas (Muller, 2007; Townsend *et al.*, 2007).

Even though restraint might generally be expected with respect to harming infants of related females, there are some well-documented cases where infanticide is directed at the offspring of close kin. For example, Hoogland (1985) reports that female colonial black-tailed prairie dogs (*Cynomys ludovicianus*) often kill offspring of close female relatives such as mothers, sisters and daughters within their own territorial group, and that their individual reproductive success is increased as a result. Infanticide of close relatives' offspring by breeding females is also reported in communally breeding species such as meerkats, where subordinate females help with rearing offspring of the dominant female (Clutton-Brock *et al.*, 1998). These examples highlight an important but commonly overlooked point that intense local resource competition between closely related individuals, as may often occur within mammalian social groups (Clutton-Brock, Albon & Guinness, 1982), can reduce the importance of indirect fitness benefits (Griffin & West, 2002; West, Pen & Griffin, 2002).

Theoretical models support the idea that female infanticide can be an important factor promoting high reproductive skew in cooperatively breeding species (Hager & Johnstone, 2004). Importantly, if females are able to discriminate their own progeny, the threat of infanticide can prevent a subordinate co-breeder from adding many young to a joint brood, so that no actual killing need occur (Johnstone & Cant 1999). Reproductive suppression in cooperatively breeding common marmosets (*Callithrix jacchus*), appears to result from reproductive restraint among subordinate females as a response to the threat of infanticide by dominant females (review in Saltzman *et al.*, 2009). Although subordinate female marmosets exhibit suppression of ovulation and inhibition of sexual behaviour, they receive little or no aggression or mating interference from dominant females, and show no physiological signs of stress. When subordinate females do attempt reproduction, in both wild and captive populations, their offspring are often killed by dominant females. By contrast, Cant *et al.* (2010) found no evidence that subordinate female banded mongooses exercise reproductive restraint to avoid eviction from cooperatively breeding groups. Since subordinate female banded mongooses tend to be evicted by the dominant female *en masse*, these authors suggest that eviction threats may be most effective in dyadic relationships and linear hierarchies where transgressors can be clearly distinguished from non-transgressors.

Although more usually associated with cooperative breeding, the threat of infanticide may also lead to reproductive inhibition among females of solitary-living species under conditions of resource limitation. For example, by hoarding food, female golden hamsters are able to stay in their nest for prolonged periods, and are able to defend their litter from potential infanticidal attacks (Huck *et al.*, 1988*a*). However, if they become food limited, females will often kill and consume their own offspring rather than leave the nest and risk infanticide by another female. Presumably this strategy allows females to retain and reuse some of their investment under threat of infanticide, rather than risk losing their litter, since intruder females have been observed to remove and consume pups (Huck *et al.*, 1988*a*).

III. WHY DO FEMALE MAMMALS COMPETE FOR ACCESS TO MATES?

Although widely overlooked in the past, the substantial evidence for resource competition among female mammals is perhaps not surprising considering the conventional assumption that female reproductive success is primarily limited by resources other than mates. More puzzling is evidence that female mammals may also compete for access to mates, either directly through aggression against receptive females or mating pairs, or indirectly through proceptive displays. Whereas mate competition between males can be explained by their relatively high potential reproductive rate, female mate competition is not predicted by this conventional logic. How then can we explain conflict between females over access to males?

(1) Access to resources provided by mates

One possibility is that males provide access to resources other than sperm for females and/or their offspring (e.g. paternal care or territorial resources) and reserve access preferentially for mating partners. If males vary in the quantity or quality of the resources they provide, females could compete for mates as an indirect manifestation of resource competition. In this case, competition may be expected to be strongest in monogamous systems, or where groups are small and exclusive, because females under these circumstances cannot freely mitigate the skew in resources held by males by settling polygynously [*cf.* the polygyny threshold model of Orians (1969)]. Consistent with this idea, women often compete for marriage partners who control access to resources, particularly in societies characterised by monogamy and strong wealth differentials among males (Campbell, 1999, 2004). However, on the basis of current evidence from other species, female mate competition in mammals appears to be primarily associated with polygynous or promiscuous mating systems with limited or no paternal care or other direct benefits provided by males (see Section III.2), rather than monogamous mating systems with a less male-biased operational sex ratio. Although this pattern could be affected by a reporting bias towards social or group-living species where there are also more opportunities for competition to be expressed, it does suggest that access to resources is not a general explanation for female mate competition in mammals. Still, under certain circumstances, competition for direct benefits provided by males may underlie female mate competition also in promiscuous mating systems, as illustrated by studies of chacma baboons. Sexually selected infanticide by unrelated males is a potential threat to offspring survival in this species, and females rely on support from male 'friends' (with which they are more likely to mate) to help protect their offspring (Smuts, 1985). Palombit, Cheney & Seyfarth (2001) found that this can result in competition between lactating females when male friends are shared, with dominant females being able to maintain higher levels of close proximity and allogrooming with preferred males when such competition occurs.

(2) Sperm limitation

Alternatively, females could be competing for limited sperm. Traditionally, limitations to male sperm supplies were thought to be unimportant for the evolution of mating strategies; however, there is now increasing awareness that this is not a safe assumption (Dewsbury, 1982; Small, 1988; Wedell, Gage & Parker, 2002). Sperm limitation can potentially result from depletion of male sperm reserves at naturalistic mating rates (e.g. Salamon, 1962; Pickett, Sullivan & Seidel, 1975; Short, 1979; Preston *et al.*, 2001) and/or adaptive male ejaculate allocation strategies (Ball & Parker, 1996; Wedell *et al.*, 2002). Although relative testis size and sperm production typically increase in response to sperm competition (Parker 1998; Ramm & Stockley, 2010), adaptive sperm allocation strategies are predicted to vary both according to sperm competition levels and male mating frequency (Parker 1998; Wedell *et al.* 2002; Parker & Ball, 2005). Thus in situations of intense sperm competition and high male mating rates, optimal ejaculate size may actually decrease as testis size and sperm production rates increase (Parker & Ball, 2005). More generally, sperm depletion may be promoted by several factors which are not reflected in the concept of potential reproductive rates. Firstly, oestrus synchronization reduces the male-bias in the operational sex ratio during the breeding season and forces males to mate at higher rates than if oestrus was asynchronous (Emlen & Oring, 1977). Secondly, multiple mating by females, whether it involves mating with several males or repeatedly with one, can promote sperm depletion by increasing male mating rates, potentially accentuated by a positive feedback (Charlat *et al.*, 2007). Finally, unanimous female mate preferences and strong male competition can push the ratio of males to females who are "qualified to mate" towards a female bias (Ahnesjö, Kvarnemo & Merilaita, 2001).

How these factors may interact to cause sperm limitation, and thereby elicit female competition, may be illustrated by the reported distribution of female mate competition among artiodactyls. Evidence indicative of female mate competition is here primarily associated with species demonstrating moderate to strong breeding synchrony (e.g. fallow deer, *Dama dama*: Schaal, 1987; topi antelopes, *Damaliscus lunatus*: Bro-Jørgensen, 2002; saiga antelopes, *Saiga tatarica*: Milner-Gulland *et al.*, 2003; red deer, *Cervus elaphus*: Bebie & McElligott, 2006). Furthermore, female multiple mating may promote sperm limitation in some of these cases. In topi antelopes, females on average mate with four (up to more than a dozen) different males during their one-day oestrus (Bro-Jørgensen, 2007*a*), and in fallow deer 20% of females may mate promiscuously (Harty, 2002). Consistent female mate preferences can also restrict the number of acceptable partners in species with female mate competition. For example, in harem-breeding red deer, where females target aggression against receptive hinds (Bebie & McElligott, 2006), females prefer large males (Charlton, Reby & McComb, 2007). Female mate competition may be promoted especially in lek systems, where females choose preferred partners on mating arenas (Bradbury, 1981; Schaal, 1987; Bro-Jørgensen, 2002). Since lek males by definition do not provide any paternal care, material benefits from males are unlikely to be the basis for female competition, which is better explained by sperm being a limiting factor. If females compete for sperm, aggression should increase mating rates, as demonstrated in topi antelopes (Bro-Jørgensen, 2007*a*).

An illuminating 'natural experiment' suggesting that sperm limitation can indeed elicit competition for fertilization comes from saiga antelope (Milner-Gulland *et al.*, 2003). Here aggressive female mate competition emerged only after the adult sex ratio became heavily female-biased following poaching. It is noteworthy that the emergence of mate competition was associated with a drastic reduction in population size, which would have alleviated rather than intensified any resource-based competition. Similarly, a study of house mice kept in a semi-natural environment found that competition among females appeared only when the number of males was experimentally reduced and oestrus cycles synchronized, again suggesting risk of not being fertilised (i.e. sperm limitation) as the trigger (Rusu & Krackow, 2004).

A low ratio of reproductively successful males to females may explain an apparent broader link between sperm limitation and polygyny. Evidence indicative of sperm limitation in polygynous primates includes a negative relationship between conception rate and the ratio of oestrous females to males in both hamadryas baboons, *Papio hamadryas* (Zinner, Schwibbe & Kaumanns, 1994) and gelada baboons (Dunbar & Sharman, 1983); in the latter case, dominant females are also reported to threaten other females who attempt to mate with the harem male (Mori, 1979). In gorillas (*Gorilla gorilla*), where males can only sustain relatively low mating rates (Short, 1979), females receive fewer copulations when other females are simultaneously in oestrus (Watts, 1990)—a finding which again suggests sperm limitation as the reason for occasional mating harassment by females (Harcourt *et al.*, 1980; Niemeyer & Anderson, 1983). In langurs (*Semnopithecus* spp.), Sommer (1989) suggested that an association between copulation harassment and uni- rather than multimale groups might be due to female competition for limited sperm. Specifically in Northern Plains gray langurs (*Semnopithecus entellus*), he found that female mating interference decreases when more than one male is present in the group.

Female mate competition is also reported from primates with multimale groups. Again, a potential explanation is that females compete for sperm because female promiscuity promotes the depletion of male sperm supplies, particularly when biased towards certain males. Thus in bonobos (*Pan paniscus*), females who interrupt mating attempts of others tend to be in oestrus themselves, and such interference is associated with increased mating rates (Hohmann & Fruth, 2003). Since female-female aggression correlates with the number of females in oestrus, but not with the number of males in the group, this suggests that female bonobos may compete for sperm from specific males. In chimpanzees, there is also evidence that females who harass mating pairs are themselves in oestrus (Nishida, 1979; Niemeyer & Anderson, 1983); moreover, female chimpanzees apparently avoid synchronizing their oestrus, which may be an adaptation to reduce competition for limited sperm (Matsumoto-Oda *et al.*, 2007). However, it is important to note that although competition for sperm may well explain female behaviour in these examples, other explanations cannot necessarily be ruled out. For example, infanticide avoidance might also be a factor contributing to female mate competition in cases where the probability of male infanticide can potentially be reduced by mating with as many males as possible, and particularly with those of high rank that pose a greater threat (Hrdy, 1979).

(3) Preventing future resource competition from the offspring of others

Rather than functioning to secure resource-rich mates or sperm, female mate competition can also potentially serve to prevent the reproduction of others in order to avoid future resource depletion. Female behaviours may in this case resemble spite (see Section IV.4), although as discussed below it can be difficult to distinguish between this and alternative functional explanations for female mate competition. Conditions favouring inhibition of others to reduce future competition are likely to be stability of social groups and limited dispersal in space, both of which increase the probability of future interactions with the offspring of current group members. Benefits of reduced future competition may therefore result from female mating interference reported in monandrous equid species, which form relatively stable harems of only moderate size (Schilder, 1990; Powell, 2008), such that future resource competition with the offspring of current group members is likely. That the offspring of other harem members in horses may constitute significant competitors is supported by evidence that lactating wild plains zebra (*Equus burchelli*) and feral female horses (*Equus caballus*) receive more aggressive bites than either pregnant or non-reproducing females (Rutberg & Greenberg, 1990; Neuhaus & Ruckstuhl, 2002, Rho, Srygley & Choe, 2004).

In common marmosets and some other cooperatively breeding species where dominant females interfere with copulations, the simultaneous presence of infanticide again suggests that the offspring of others may constitute competitors for future resources (Saltzman *et al.*, 2009), and hence that mating interference might function to reduce future competition as well as to secure additional investment from helpers (see Section II.3). Female aggression has also been related to mating activities in carnivores such as wolves, *Canis lupus* (Rabb, Wooply & Ginsburg, 1967; Zimen, 1976) and wild dogs (Frame *et al.*, 1979), both cooperatively hunting canids living in stable packs. In wolves, aggression between females is particularly intense with a peak during the breeding season, and in both wolves and wild dogs, dominant females are reported to prevent the courtship of subordinates, in effect monopolising reproduction. Such behaviour is again compatible with a function of preventing future resource competition, as well as securing investment in the dominant females own young from helpers (see Section II.3); competition for sperm appears less likely in these examples since mating rates are not particularly high.

However, more direct evidence in support of the idea that female competition for mates functions to reduce future resource competition is currently lacking for these and other species.

IV. FEMALE COMPETITIVE STRATEGIES

(1) What determines female competitive ability?

As in males, aggressiveness and physical strength can be important determinants of competitive success among female mammals, and there is evidence that female dominance may often be correlated with age or body size. For example, older and larger females consistently dominate younger and smaller ones within stable social groups of feral ponies (Rutberg & Greenberg, 1990), and African elephants (*Loxodonta africana*: Archie *et al.*, 2006), and the highly linear and stable social hierarchy of female mountain goats is strongly correlated with age (Côté, 2000). Similarly, dominance relations among wild female chimpanzees (Pusey *et al.*, 1997) and captive female bottlenose dolphins (*Tursiops truncatus*: Samuels & Gifford, 1997) are age related, although rates of female agonism in both species appear generally low. To some extent, stable age-related relationships may be explained by dominance relations established early in life being perpetuated between familiar individuals, as demonstrated in red deer, since older hinds are much more likely to lose interactions, and younger hinds to win, when outside their normal home ranges (Thouless & Guinness, 1986). It is important to recognise that dominant females may also attain larger body size because they are high ranking and have access to better quality resources. Nonetheless, experimental studies indicate that body mass prior to introduction predicts subsequent dominance rank and breeding success of female house mice (Rusu & Krackow, 2004). Similarly, in cooperative breeding meerkats, the probability of acquiring a breeding role depends partly on body mass in relation to competitors, both at the time of dominance acquisition and early in life (Hodge *et al.*, 2008). In highly social species such as primates, females may also rely on support from others to establish and maintain their dominance status so that traits such as age and body size can be less important predictors of dominance. For example while dominance relations among gelada baboons depend on individual aggressiveness, this is modified by coalitionary support from female relatives, and female relatives rank adjacent to each other in dominance more often than expected by chance (Dunbar, 1980). Maternal rank also appears to be inherited in spotted hyenas and so remains relatively stable over time (Frank, 1986; East *et al.*, 2009). Hence, although older females typically have higher dominance rank within a lineage, neither body size nor age is a strong predictor of dominance when comparing across competing matrilines (Frank, 1986).

Particularly in cooperatively breeding species where reproductive opportunities are limited, dominant females may undergo physical changes associated with their status (O'Riain *et al.*, 2000; Russell *et al.*, 2004). Female meerkats that acquire dominant status increase in body mass and have higher levels of circulating testosterone during pregnancy, as well as higher rates of aggression than subordinates (Clutton-Brock *et al.*, 2006). More generally however, the role of circulating androgen levels in determining female dominance status is not straightforward. For example, neither the aggression rates of female ring-tailed lemurs nor the proportion of same-sex individuals they dominate are significantly correlated with individual androgen levels (von Engelhardt Kappeler & Heistermann, 2000). Similary, although the rock hyrax (*Procavia capensis*) is the only species to date for which females have been reported both to dominate and have higher testosterone levels than males, female testosterone levels are apparently not significantly correlated with rank (Koren, Mokady & Geffen, 2006). There is some evidence though that circulating hormone levels might influence the competitive ability of offspring *via* maternal effects. Androgen levels in wild spotted hyenas are higher during late gestation in dominant females than in subordinate females, and cubs born to mothers with high androgen levels exhibit higher rates of aggression (Dloniak, French & Holekamp, 2006).

Females may also use armaments in intrasexual competition. Although ungulate horns and antlers are thought to owe their evolutionary origin primarily to their role in male combat, these weapons are also often found in females where they may be used against predators and/or in female competition (Packer, 1983; Roberts, 1996; Stankowich & Caro, 2009). Direct evidence that female weaponry is beneficial under resource competition comes from studies of female caribou, *Rangifer tarandus* (Barrette & Vandal, 1986; see also Holand *et al.*, 2004*a*). When competition for limited and patchy food resources becomes particularly intense during the winter months, female caribou with larger antlers are more successful in obtaining access to limited food (Barrette & Vandal, 1986). Moreover, in a study of domestic cattle (*Bos taurus*) in which female horns were experimentally removed, it was concluded that horns are of major importance in determining dominance relationships within newly established social groups (Bouissou, 1972). Natural variation in the presence of horns occurs in female Soay sheep (*Ovis aries*), due to a polymorphism in horn development, and Robinson & Kruuk (2007) found that females with horns are more likely to initiate and win aggressive interactions, particularly when local resource competition is intense. Female armaments can also be used in mate competition. Female aggression directed at mating pairs is more common in ungulates with limited sexual dimorphism (e.g. equids: Powell, 2008; topi antelopes: Bro-Jørgensen, 2002), which might be explained by the fact that such females are relatively well-armed. By contrast, in sexually dimorphic species where females are poorly armed in comparison to males, any female aggression in relation to mating is typically directed at other females only (e.g. saiga antelopes: Milner-Gulland *et al.*, 2003; fallow deer: Schaal, 1987; red deer: Bebie & McElligott, 2006). Still, the results of recent comparative analyses of bovids suggest that in general, the selective advantage of female horns does not come from mate competition (Bro-Jørgensen, 2007*b*), but rather from their use against predators and, to a lesser extent, in territorial defence (Stankowich & Caro, 2009).

(2) What is the role of signalling in female competition?

While the role of conspicuous signals in male mating competition is well established (Darwin, 1871; Andersson, 1994), similar signals expressed by females have traditionally been assumed to represent a correlated response to sexual selection acting primarily on males (Lande, 1980). More recently though, it has been demonstrated that ornamentation of female birds can evolve independently of selection on males (Amundsen, 2000), that ornaments can signal female quality (Roulin *et al.*, 2000; Jawor *et al.*, 2004) and that females with larger ornaments may obtain more sperm from preferred males (Cornwallis & Birkhead, 2007). It has also recently been demonstrated that increased female competition in cooperatively breeding species can result in more ornamented females and therefore less sexual dimorphism (Rubenstein & Lovette, 2009).

Limited available evidence for mammals suggests that if females do use signals in competing to attract preferred males, these are most likely to function in advertising fertility and sexual receptivity. For example, the facial colouration of female mandrills (*Mandrillus sphinx*) (Setchell, Wickings & Knapp, 2006*b*) and rhesus macaques (*Macaca mulatta*) (Dubuc *et al.*, 2009) is brighter during the fertile phase of the oestrous cycle, and the copulatory calls of female baboons and macaques also change predictably in relation to oestrous stage, again revealing the most likely time of ovulation (O'Connell & Cowlishaw, 1994; Semple & McComb, 2000; Semple *et al.*, 2002). Accordingly, male mammals are expected to pay particular attention to indicators of female ovulation and receptivity due to the relatively narrow window of peak fertility in most species. Semple (1998) found that female Barbary macaques (*Macaca sylvanus*) attract more males and receive more copulations from higher ranked males when they give copulation calls. In playback experiments, males also discriminated between copulation calls given by females at different stages of their ovulatory cycle by approaching the calls of females in late oestrus more often (Semple & McComb, 2000). Pradhan *et al.* (2006) suggest that the function of copulation calls varies among species, serving to attract dominant males in species with effective mate-guarding, and to elicit sperm competition in species with ineffective mate-guarding.

Other aspects of female reproductive value, such as fecundity and maternal experience, may be more accessible to direct assessment by males than receptivity, for example on the basis of body size (Solomon, 1993; Preston *et al.*, 2005) or age-related traits (Muller, Thompson & Wrangham, 2006; Szykman *et al.*, 2007). However, signalling might sometimes be used to reinforce information also in this case, for example the facial colouration of female mandrills increases significantly with age, and primiparous females are darker than multiparous females (Setchell *et al.*, 2006*b*). Evidence that female mammals signal other components of their quality or condition to potential mates is limited. Horn size of female buffalo (*Syncerus caffer*) has been suggested as an honest indicator of health and quality, since infection with multiple parasites was found to correlate with smaller horn size, and females with larger horns were in better condition and significantly more likely to be lactating (Ezenwa & Jolles, 2008); however, any signal function remains to be documented.

It is not always clear whether receptivity or individual quality is being signalled to potential mates, and here the function of exaggerated sexual swellings found in some Old World primates has been the subject of particular controversy (Dixson, 1983, Hrdy & Whiten, 1987; Nunn, 1999; Zinner *et al.*, 2004). Pagel's (1994) reliable indicator hypothesis postulates a central role for female competition in the evolution of sexual swellings. According to this hypothesis, females living in multimale groups advertise their quality in order to attract the best males and to inhibit reproduction in other females by monopolising available sperm reserves. Support for the reliable indicator hypothesis comes from Domb & Pagel's (2001) study of baboons (*Papio anubis*), in which females with larger swellings reproduced earlier, had higher birth rates, produced a greater proportion of surviving offspring and stimulated higher levels of competition among males.

Domb & Pagel's (2001) study has subsequently been criticised (Zinner *et al.*, 2002; see also Zinner *et al.*, 2004), and several later studies failed to find evidence that sexual swellings reliably indicate female quality in baboons or other species (Deschner *et al.*, 2004; Setchell & Wickings, 2004; Setchell *et al.*, 2006*a*; Higham *et al.*, 2008, see also Nunn, van Schaik & Zinner, 2001). However, various studies have found that swellings may advertise the quality of a particular cycle or cycle phase (e.g. Emery & Whitten, 2003; Deschner *et al.*, 2004; Gesquiere *et al.*, 2007), a factor that could be important in competition for mates. Moreover, a recent study on chacma baboons indicates that although swellings are fertility indicators, they appear to have been modified by selection also to act as signals of individual quality (Huchard *et al.*, 2009). This study found that females in better condition had larger swellings and higher reproductive success, and were preferred as mates by males. The reliable indicator hypothesis is intuitively appealing as an explanation for the evolution of extreme sexual swellings because its emphasis on competitive interactions could potentially account for the exaggeration of the trait (see Pagel, 1994). Although other plausible attempts have been made at explaining why sexual swellings should have become so exaggerated (e.g. Nunn, 1999; Nunn *et al.*, 2001; Higham *et al.*, 2009), the reasoning involved seems less compelling in the absence of some clearly defined conflict of interests, promoting escalation between competing signallers (Pagel, 1994), or sexually antagonistic coevolution between signaller and receiver (see also Dixson, 1998).

Several studies in other taxa highlight the importance of resource competition, rather than mate competition, as a potential selection pressure for female signal evolution (LeBas, Hockman & Ritchie, 2003; Heinsohn, Legge & Endler, 2005; LeBas, 2006). In the mammalian literature, examples where conspicuous visual signals are used in competition for resources between females are currently more limited. Nonetheless, it seems likely that female mammals may often signal their competitive ability in the context of resource competition *via* olfactory or other signals. Flank marking by female golden hamsters and urine marking by female house mice are each apparently related to aggressive motivation and intrasexual competition (Hurst, 1990; Palanza, Parmigiani & vom Saal, 1994; Johnston, 2008), and the scent-marking behaviour of female ring-tailed lemurs and golden lion tamarins may also serve a function in intergroup competition (Miller, Laszlo & Dietz, 2003; Mertl-Millhollen, 2006; Scordato & Drea, 2007).

(3) Why aren't competing females more overtly aggressive or flamboyant signallers?

Although there are well-documented cases of overt (and occasionally fatal) aggression among females (e.g. Niemeyer & Anderson, 1983; Packer *et al.*, 1988; Lacey & Sherman, 1997; Bro-Jørgensen, 2002; Campbell, 2004; Pusey *et al.*, 2008), aggressive encounters appear to be generally more low-key than in males, except in the context of offspring defence (Maestripieri, 1992). Similarly, as discussed above (Section IV.2), examples of costly or flamboyant competitive signalling appear to be less common among female mammals than among males. So why do competitive traits appear to be more modest in female mammals than in males? A crucial reason appears to be that competitive traits only have scope to yield relatively low instantaneous benefits in females, due to their lower potential reproductive rate (Clutton-Brock & Vincent, 1991), and therefore have to be sustained for longer in order to secure benefits comparable to those of males. Thus because males, unlike females, can often obtain considerable reproductive success over a short time span, even high costs of extreme adaptations to fighting or signalling can lead to positive pay-offs (Carranza *et al.*, 2004). Exacerbating the lower potential for female competitive traits to provide high instantaneous pay-offs, females may also incur higher costs of intense competition due to a direct trade-off with offspring production. Hence, investment in exaggerated sexually selected traits may divert resources away from producing and rearing offspring (Chenoweth, Doughty & Kokko, 2006; Fitzpatrick, Berglund & Rosenqvist, 1995; LeBas, 2006), and higher costs of sexually selected traits in females have been suggested by several authors. For example, Campbell (1999, 2002) emphasises the importance of high maternal investment and infant dependence as factors that should constrain aggression among women to minimise risk of injury, and Packer *et al.* (1995) argue that elevated levels of androgens associated with high dominance rank might affect female fertility.

Cooperative strategies for competing might also explain to some extent why weaponry used for direct combat is less exaggerated in females of some species compared to males. As an example, comparative evidence indicates that female weaponry (canine teeth) is less developed in primate species where females regularly form coalitions (Plavcan, van Schaik & Kappeler, 1995). Examples of cooperation between females in this context typically involve coalitions between related individuals engaging together in territory defence or subordination of rival lineages (Section II.2). Here, cooperation in competing for limited resources could reduce the risk of engaging in escalated aggression for each individual involved. Cooperation might be a particularly beneficial strategy to secure access to renewable resources that can be used to promote the survival and reproductive success of matrilineal descendants, since the benefits of monopolising such resources are potentially great, but, unlike mates monopolised by males, cannot be immediately utilised by a single individual. Current adaptations for cooperation might also reflect resolution of competition in previous evolutionary history, as recently suggested to explain menopause in humans and cetaceans as 'the ghost of reproductive competition past' (Cant & Johnstone, 2008). Females of the younger generation are proposed to be competitively superior to the older generation due to relatedness asymmetries that emerge in families when adult females disperse, and therefore older females may do better by helping to raise offspring of relatives.

(4) Why do female competitive interactions sometimes appear spiteful?

An individual that is willing to incur a fitness cost in order to inhibit the reproductive success of a competitor may be described as behaving spitefully (Hamilton, 1970; Gardner & West, 2004). The evolution of spiteful behaviour can be favoured by kin selection under certain conditions where competition is local (e.g. within a social group) and where spite is directed at those of lower than average relatedness to the spiteful individual compared to other competitors. Such 'Hamiltonian spite' is hence most likely to be favoured in situations where individuals interact with both kin and non-kin (and can distinguish between them) in highly competitive environments, and may be more common than previously appreciated (Gardner & West, 2004). An alternative, although not necessarily mutually exclusive, explanation of apparently spiteful behaviour is that it is actually a form of indirect altruism (also known as 'Wilsonian' spite—Gardner & West, 2004). That is, by inhibiting the reproductive success of a competitor at some cost to itself, an individual may ultimately benefit by gaining indirect benefits for its relatives, for example by reducing future competition. Thus while Hamiltonian spite relies on negative relatedness to the victim, Wilsonian spite relies on positive relatedness to beneficiaries.

Inhibition of competitors' reproduction by female mammals might be regarded as spiteful in either (or both) senses outlined above, particularly in cases where resources do not appear to be a limiting factor at the time when such behaviour is observed. For example, Dunbar (1980) noted that dominant female gelada baboons harass subordinates even though they do not seem to be competing for any specific resource. Similarly, Wasser & Starling (1988) found that coalition attacks by female yellow baboons peaked during periods of maximum food availability, and hence concluded that such attacks did not appear to function primarily as a means of directly acquiring resources. Dominant female elephant seals (*Mirounga leonina*) have been reported to harass and attack pups of subordinates, again in the absence of any obvious resource competition (McCann, 1982), and some ground squirrels (*Spermophilus beechyi, S. columbianus*) kill litters of other females but do not necessarily gain access to their burrow or territory (Balfour, 1983; Hare, 1991; Trulio, 1996). Examples of mating interference can also look like spite, since reports exist where it seems unlikely that sperm are a limiting resource (see Section III.3). Related to this, multiple mating and/or sexual advertisements have been suggested to have a spiteful function in female competition by depleting male sperm reserves to reduce the fitness of other females (Small, 1988; Petrie, 1992; Pagel, 1994).

Contrasting levels of parental investment between the sexes may ultimately explain why female competitive interactions sometimes appear spiteful compared to those of males (see Table 2). Female mammals typically have high levels of parental investment and relatively low potential reproductive rates, and much of the variance in their reproductive success can often be explained by differences in the survival and reproductive success of their offspring (Section V.I). In some cases, this can lead to benefits of preventing the reproduction of others, specifically when such inhibition increases the probability of offspring survival and reproduction for the suppressor due to the operation of density-dependent population regulation (e.g. Wasser & Barash, 1983; Wasser & Starling, 1988). By contrast, male mammals typically have low parental investment and high potential reproductive rates, such that variation in their reproductive success is closely linked to differences in mating success (e.g. Clutton-Brock, 1988). The relative contribution of males to the next generation should therefore often depend largely on the number of offspring they sire, regardless of whether populations are regulated by resource limitation and density-dependent mortality. Hence although certain male reproductive strategies such as infanticide or mate guarding can result in the inhibition of competitors (Table 2), these are typically assumed to provide some immediate reproductive benefit such as increased mating or fertilisation success, and a function in reducing future competition for offspring appears less likely.

V. FEMALE COMPETITION AND SEXUAL SELECTION

(1) Variance in fitness resulting from female competition

For species with polygynous and promiscuous mating systems, it has often been assumed that variance in reproductive success (and hence the potential for selection) should be greater for males than for females (e.g. Payne, 1979, review in Hrdy & Williams, 1983; Clutton-Brock, 1988; but see Sutherland, 1985; Grafen, 1988). This expectation is linked to Bateman's influential experimental study of *Drosophila melanogaster*, which revealed significantly greater variance in mating success (and hence reproductive success) among males than females under laboratory conditions Bateman 1948). Extrapolation from that study has even led some authors to conclude that females in natural populations should have essentially similar reproductive success, with each breeding at or close to the limit of their reproductive capacity (e.g. Daly & Wilson, 1978, reviewed in Clutton-Brock, 1988). More recently though, limitations of Bateman's study have been emphasised, particularly in the context of understanding female reproductive strategies (Hosken & Stockley, 2003; Dewsbury, 2005; Drea, 2005; Tang-Martinez & Ryder, 2005; Snyder & Gowaty, 2007; Carranza, 2009). Moreover, a growing number of field studies have revealed evidence of quite substantial variation in reproductive success of female mammals in natural or semi-natural populations during the period of observations (Clutton-Brock, 1988; Schulte-Hostedde, Millar & Gibbs, 2004; Clutton-Brock *et al.*, 2006; von Holst *et al.*, 2002; Hauber & Lacey, 2005).

The most dramatic examples of reproductive skew among female mammals are found in species with singular cooperative breeding systems, where, unusually, skew in the number of offspring produced by females is often greater than that of males (Hauber & Lacey, 2005; Clutton-Brock *et al.*, 2006). Much of the variation in female reproductive success within such systems can be explained at a proximate level by mechanisms of reproductive suppression or restraint among subordinate females (Section II.3). Direct evidence that competition for reproductive opportunities within such systems is ultimately resource-based comes from experimental studies of dwarf mongooses (*Helogale parvula*) in the field, demonstrating that subordinate females are more likely to become pregnant when receiving supplementary food (Creel & Waser, 1997). Similarly, subordinate female meerkats are more likely to breed when resources are abundant (Clutton-Brock *et al.*, 2001).

In contrast to the extreme reproductive skew reported for females in species with singular cooperative breeding systems, skew in female reproductive success (at least in terms of offspring numbers) is typically less dramatic in other mammal species studied so far (Table 3; Hauber & Lacey, 2005). As expected, available evidence for polygynous and promiscuous species indicates that variation in lifetime breeding success is typically lower for females than for males (Table 3; Hauber & Lacey, 2005). However, it is important to stress that variation in female reproductive success in the relatively few species studied to date is by no means insubstantial. For example, only about 50% of female wild European rabbits (*Oryctolagus cuniculus*) studied by von Holst *et al.* (2002) achieved any reproductive success under semi-natural conditions (varying between one and

Table 2. Types of intrasexual competition favoured by different reproductive strategies in relation to parental investment. Reproductive strategies associated with low parental investment (usually male) typically lead to competition for mating opportunities to maximise offspring numbers. By contrast, reproductive strategies associated with high parental investment (usually female) often favour competition to promote the survival and reproductive success of descendants, as well as to maximise offspring production rates (for simplicity, strategies for promoting the survival and reproductive success of relatives other than direct descendants are not considered here)

	Reproductive strategies → Intrasexual competition					
	Low parental investment (male)			High parental investment (female)		
Offspring production	Maximise number of offspring with minimal parental investment in each	→	Competition for mates and/or fertilisations	Maximise number of offspring with optimal parental investment in each	→	Competition for resources needed for own reproduction, competition for mates if gametes limiting
Mate choice	Choose mates to maximise offspring production	→	Competition for favoured mates if fecundity is variable	Choose mates to promote offspring survival and/or reproductive success	→	Competition for mates if gametes of favoured mates are limited, or (indirectly) for resources if access controlled by mates
Resource monopolisation	Monopolise resources to maximise offspring production	→	Competition for resources required by potential mates if monopolisation leads to increased mating opportunities	Monopolise resources to achieve optimal offspring production, and/or to promote survival and reproductive success of descendants	→	Competition for resources needed for own reproduction; competition for more resources than required for own reproduction; lineage competition
Inhibition of competitors	Inhibit reproduction of competitors to maximise offspring production	→	Competition for mates (e.g. *via* infanticide) and/or fertilisations	Inhibit reproduction of competitors to achieve optimal offspring production, and/or to promote survival and reproductive success of descendants	→	Competition for resources needed for own reproduction; competition for more resources than required for own reproduction; lineage competition

Table 3. Estimates of variance in reproductive success for male and female mammals based on offspring production. Standardised variance in reproductive success (St. Var.) is defined as variance in reproductive success divided by the square of mean reproductive success ($\sigma^2 / \bar{x}^2$) and estimates the opportunity for selection on the two sexes. Values are averaged across cohorts

Species	Estimate of reproductive success	Male St. Var	Female St. Var	Male/Female St. Var	Source
Red deer *Cervus elaphus*	Number of offspring surviving to 24 months produced over lifetime by animals that reached breeding age	1.43	0.36	3.97	Clutton-Brock *et al.* (1988)
Meerkat *Suricata suricatta*	Number of offspring surviving to 12 months produced during tenure of dominant subjects	3.98	6.13	0.65	Clutton-Brock *et al.* (2006)
Lion *Panthera leo*	Number of offspring surviving to 12 months produced over lifetime by breeding individuals	1.12	0.41	2.73	Packer *et al.* (1988)
Northern elephant seal *Mirounga angustirostris*	Number of offspring surviving to weaning age produced over lifetime by breeding individuals	21.77	5.23	4.16	LeBoeuf & Reiter (1988)
Human *Homo sapiens*	Number of offspring surviving to 21 years produced over lifespan by breeding individuals	0.52	0.25	2.08	Borgerhoff Mulder (1988)
Yellow-pine chipmunk *Tamias amoenus*	Number of weaned offspring produced per breeding season by breeding individuals	1.24	0.93	1.33	Schulte-Hostedde *et al.* (2004)

nine adult offspring), and the mean reproductive lifespan and lifetime fitness of females that achieved high social rank at an early age was approximately 60% greater than that of lower ranking females. Moreover, in a natural population of yellow-pine chipmunks (*Tamias ameonus*), Schulte-Hostedde *et al.* (2004) found that variance in reproductive success was not significantly different between males and females, and concluded that the opportunity for sexual selection was only marginally higher in males than in females. Thus, based on the empirical evidence, it appears that even if males have higher potential reproductive rates, various constraints can result in females having similar or greater variance in actual reproductive rates, and it is actual rather than potential reproductive rates which, when linked to heritable competitive traits, determine the strength of selection (Kokko & Monaghan, 2001). Generally, it is also worth noting that, when it comes to empirical measurements of the variance in actual reproductive rates, short-term studies tend to yield overestimates for males, who are often 'king-of-the-hill' only for a limited period (e.g. Rasmussen *et al.*, 2008), and underestimates for females, where variation in individual lifespan and offspring survival is often more important and where reproduction of descendants should also be considered (see below).

It is also important to emphasise that female competition can generate variation in offspring quality as well as quantity (Table 2). For example, by competing for copulations with preferred males, females may affect offspring fitness through direct material benefits and/or indirect genetic benefits (e.g. Byers & Waits, 2006). Resource competition can also have important consequences for the long-term reproductive success of female mammals by affecting levels of maternal investment. This can explain variation in the quality rather than (or in addition to) the quantity of offspring produced, and hence their subsequent survival and reproductive success. For example, differences in offspring survival after weaning are the principal source of variation in reproductive success among breeding females in species such as red deer (Clutton-Brock *et al.*, 1988) and vervet monkeys (Cheney *et al.*, 1988). Furthermore, maternal investment can have important consequences for offspring reproductive success, particularly among polygynous species such as red deer where male mating success is strongly influenced by body size and/or condition (Clutton-Brock, 1988). Here, from a multigenerational perspective, females might be viewed as competing for mates *via* their sons, with consequences for the evolution of life-history traits such as body size, growth rate and litter size (Carranza, 1996). Long-term fitness consequences of female competition are also likely to result where territories or dominance rank are inherited (Blomquist, 2009; East *et al.*, 2009), or more generally where offspring fitness is influenced via persistent maternal effects (e.g. Altmann & Alberts, 2005; Dloniak *et al.*, 2006; Onyango *et al.*, 2008). We should not expect that such competition to increase the quality (traditionally considered typical of females) rather than quantity (traditionally considered typical of males) (Andersson, 1994) of offspring necessarily leads to weaker selection. If reproduction is highly skewed towards high-quality individuals, the quality of offspring may matter more than quantity, and when only females can affect offspring quality, notably through maternal effects, selection may be strongest in females.

In conclusion, available evidence suggests that the reproductive success of female mammals can be highly variable within natural populations. Moreover, it is important to emphasise that fundamental differences in the reproductive strategies of males and females (Table 2) complicate attempts to compare variance in their reproductive success. That is, while the outcome of male competition for mates can be quantified in a relatively straightforward way by comparing the number of offspring sired, the fitness consequences of female competition for resources may only become apparent over much longer time scales, with diffuse consequences for inclusive fitness (including effects on both offspring quality and numbers) potentially spanning several generations. Hence, establishing the true extent of variation in female fitness which results from intrasexual competition remains an important challenge, and the influence of female competition as an evolutionary selection pressure may have been significantly underestimated to date.

(2) The role of female competition in sexual selection

The evidence that we have presented so far indicates that competition among female mammals is common and can potentially have significant fitness consequences. In this final part of the review, we discuss the conditions under which female competition results in sexual selection, according to various definitions proposed for the term. In the discussion we use the term natural selection in its broadest sense, i.e. as encompassing both sexual and non-sexual selection (Endler, 1986; Clutton-Brock, 2004).

(*a*) *Does female competition for mates result in sexual selection?*

We begin by considering probably the most widely accepted definition of sexual selection, as resulting from differential mating or fertilisation success (Andersson, 1994). For females, this might occur in situations where sperm are a limiting resource for which they must compete in order to achieve their optimal reproductive rate (Table 2). The evidence reviewed in Section III indicates that sperm limitation may be currently underestimated within polygynous and promiscuous mating systems, where successful males can suffer sperm depletion. Consequently, females may have to compete for mating opportunities, particularly where they have a limited timeframe in which to conceive (Bro-Jørgensen, 2007*a*). Since these scenarios involve competition for mates, it seems reasonable to describe the differential mating success that results as potentially resulting in sexual selection on females. When females compete for the sperm of favoured males, they are not competing for reproductive opportunities *per se*, since alternative mates are available. Nonetheless, such competition could still potentially lead to the evolution of exaggerated female signals to attract preferred mates or adaptations for contest competition that are directly analogous to sexually selected traits in males (Section IV.2).

Applying the established definition of sexual selection is less straightforward when we consider examples in which the ultimate function of female competition for mates appears related to resource acquisition. This is apparently not unusual, since examples of mating interference by females can often be explained as attempts to inhibit the reproduction of rivals rather than to secure access to limited sperm reserves (Section III.3), and females may also compete for males that control access to valuable resources or provide protection (Section III.1). Following Wade & Arnold (1980), sexual selection is often operationally defined as selection arising from variance in mating success, which, if applied to females, could include the outcome of mating interference which functions in resource competition. Here, selection resulting from variance in mating success is defined as sexual selection, regardless of the ultimate function of the behaviour that leads to such variance. This definition captures Darwin's distinction between natural and sexual selection when applied to males (as originally specified by Wade & Arnold, 1980), including examples where competition for resources translates into differential mating success (Fig. 1). However, the distinction between natural and sexual selection appears less clear in the reverse scenario for females, where competition for mates translates into differential access to resources (Fig. 1).

(*b*) *Does female competition for resources other than mates result in sexual selection?*

A clear distinction between natural and sexual selection is even more difficult to achieve in the context of direct competition for resources other than mates. Here, we can consider employing a broader definition of sexual selection, as the advantage that some individuals have over others of the same sex and species in exclusive relation to reproduction. Do examples exist where competition for resources among females has consequences only for their reproductive output? In theory this certainly seems plausible, but in most cases the distinction with natural selection is blurred because resources are also important for the females' own survival and maintenance, which in turn promote long-term reproductive success (Table 2). It has recently been suggested that a broader definition of sexual selection can be usefully interpreted as encompassing the consequences of resource competition among females where reproductive opportunities are limited (Clutton-Brock, 2004, 2009; Clutton-Brock *et al.*, 2006). Sexual selection could thus be regarded as arising from reproductive competition between members of the same sex (rather than arising strictly from mating competition), which would include selection for resources that allow individuals to reproduce, as well as selection operating through variation in fecundity that is related to social rank (Clutton-Brock, 2004). This approach seems most useful in cases where there is relatively conspicuous skew among females in the number of offspring produced. Nonetheless, even in such cases it can be

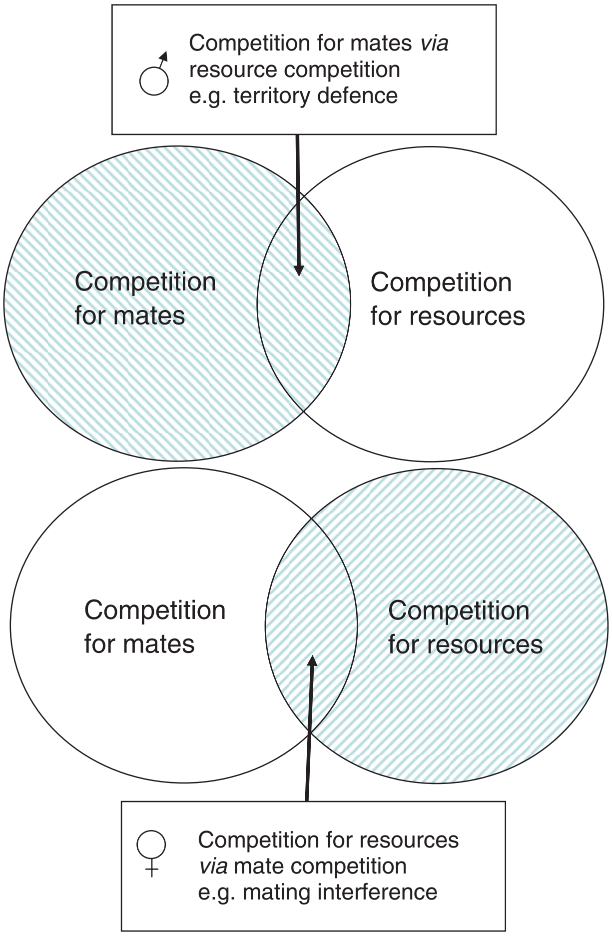

Fig. 1. Competition for mates and for resources overlaps to some extent within both sexes. Whereas males typically compete for mates (upper hatched area), they may also compete for resources that provide access to mates. Hence in some cases, male competition for resources at a proximate level may ultimately function to secure mating opportunities. Similarly, whereas females typically compete for resources (lower hatched area), they may also compete for mates that control resources, or interfere with mating opportunities of others in order to secure access to future resources for themselves and/or for their descendants. Hence in some cases, female competition for mates at a proximate level may ultimately function to secure resources. This can be problematic when applying traditional definitions of sexual selection to females (see main text). The relative sizes of the areas are arbitrary.

difficult to distinguish between natural and sexual selection, according to established definitions (Clutton-Brock, 2009). Hence Clutton-Brock (2004) also argues that there may be a case for abandoning the distinction between natural and sexual selection altogether, and focusing instead on comparing the selection pressures operating on males and females.

(*c*) *Intrasexual competition and sex-dependent selection*

As discussed above, under established definitions based on mating competition, the influence of female competition in the sexual selection of mammals is mainly restricted to cases where females compete for sperm of favoured (or competitively successful) males. More broadly though, selection may often result from intrasexual competition to acquire resources other than sperm and can result in diverse competitive strategies (Table 2). Although not consistent with established definitions of sexual selection, the selection that results from these additional forms of intrasexual competition might be usefully regarded as a type of sex-dependent selection (i.e. any selection process which operates differently in the two sexes), as defined by Carranza (2009). This broader definition builds on the assumption that wherever the sexes differ in biology, the difference is ultimately a consequence of their strategies for securing success in reproduction. The concept of sex-dependent selection is particularly appealing in the present context because the prospect of identifying similarities and differences in selective pressures between the sexes appears more feasible than attempting to tease apart the relative impact of selection for reproduction and survival, particularly in females. Classical sexual selection (based on competition between mates) may thus be regarded as a subset of sex-dependent selection or selection in relation to sex (Fig. 2). Similarly, West-Eberhard (1983) viewed sexual selection as a subset of social selection, broadly defined as selection resulting from ‘competition in which an individual must win in contests or comparisons with conspecific rivals in order to gain access to some resource, including (under sexual selection) mates’. As presented in Fig. 2, both sex-dependent selection (Carranza, 2009) and social selection (West-Eberhard, 1983) provide a broader theoretical framework for studies of intrasexual competition, beyond traditional definitions of sexual selection, thus placing much greater emphasis on the importance of competition between females.

VI. FUTURE STUDIES

The causes and consequences of female competition in long-lived, complex organisms such as mammals offer an exciting but challenging research focus, where much remains to be uncovered. In many cases the processes involved are likely to be distinct from, and less conspicuous than, those shaping male competitive strategies. Thus, important selection on females may arise from competition for mating opportunities or resources that are not immediately limiting to their own fertility or fecundity but instead promote the survival or reproductive success of their descendants, sometimes through subtle consequences for offspring quality (Table 2). A multigenerational perspective is ideally required to clarify the ramifications of female competition in such cases. Here, long-term studies combining behavioural and genetic analyses can provide valuable data on the costs and benefits associated with female strategies. In particular, the often puzzling question as to whether female mate competition is elicited by sperm limitation or benefits arising from depressing the reproductive success of others might be

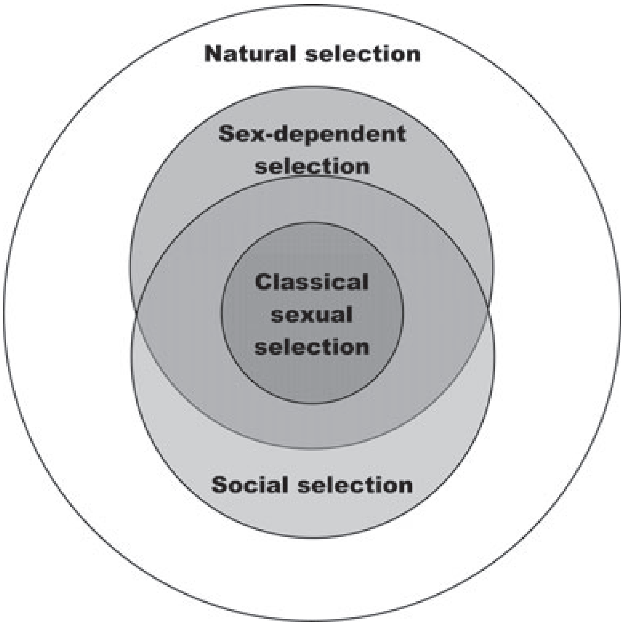

Fig. 2. Relations between natural, sex-dependent, social and sexual selection. Sexual selection is here regarded as a subset of natural selection in the broad sense (following Endler, 1986) and is defined as selection arising from competition for mates or fertilisations (Andersson, 1994). Sex-dependent selection is defined as 'those natural selection forces that operate differently in males and females because of the strategies of the sexes' (Carranza, 2009—see also Table 2). Social selection is defined as resulting from 'competition . . . with conspecific rivals in order to gain access to some resource, including (under sexual selection) mates' (West-Eberhard, 1983). Most examples of female competition reviewed here fall within the area of overlap between sex-dependent and social selection, and only a relatively small subset of these examples may be regarded as resulting in sexual selection as traditionally defined. This shows how a broader perspective is needed to understand the evolutionary causes and consequences of female competition. The relative sizes of the areas are arbitrary.

targeted in this way. Over longer evolutionary time scales, it is also possible that selection arising from female competition may not only cause direct selection on competitive traits in females, but also indirect selection on other traits, sometimes in males as well as females (*cf.* Carranza & Pérez-Barbería, 2007).

A further important focus for future research will be to determine how ecological, socioecological, and life-history factors interact to influence the form and relative intensity of female reproductive competition within and across species. Probably in part due to the more arduous data collection involved, we currently know little about the prevalence and function of female competition in solitary and pair-bonding mammals in comparison to gregarious and group-living species. Monogamous mammals are of special interest since female competition for high-quality mating opportunities could be particularly strong in this case. Similarly, studies of solitary species, although more challenging, promise to reveal entirely different strategies for conflict resolution in comparison to more gregarious species (e.g. Pemberton & Renouf, 1993). A focus on relatively conspicuous forms of competition also means that we know more about species utilising resources that are clumped or defendable, particularly primates (Sterck *et al.*, 1997; Emery Thompson, Stumpf & Pusey, 2008) and cooperatively breeding carnivores (Clutton-Brock *et al.*, 2006), and less about inconspicuous competitive interactions between females such as those involving scramble competition and avoidance (e.g. Kaufmann, 1983; Thouless, 1990; Isbell, 1991; Sterck *et al.*, 1997; Knott *et al.*, 2008), or competitive scent marking (e.g. Snowdon, 2004; Drea, 2005, Johnston, 2008). A research bias towards larger, diurnal species may also explain why species-rich groups such as bats and rodents, together with marsupials, are currently understudied. However, resource competition in small mammals is of considerable interest due to the often high energetic demands of reproduction in these species (Speakman, 2008). Investigation of more diverse mammalian taxa might also reveal conditions under which competition is typically low or negligible. For example, female bottlenose dolphins are gregarious but display little evidence of aggression, apparently because they neither compete for nor share food (Scott *et al.*, 2005).

Future studies are also needed to illuminate the ecological and social factors which favour female cooperation, including the role of environmental harshness and temporal variability in promoting cooperative breeding, and the degree of reproductive skew tolerated, given that suppressed individuals may have fewer alternative options in adverse environments (Rubenstein & Lovette, 2007). Another outstanding question of fundamental evolutionary importance is the function of apparently spiteful behaviour. Of particular interest would be to determine whether inhibiting the reproduction of others can lead to indirect fitness benefits *via* reduced competition, and to identify cases where pure 'Hamiltonian' spite might be invoked to explain inhibition of competitors' reproduction (see Gardner & West, 2004). The distribution of both cooperative and spiteful strategies is likely to be influenced by differences among species in their ability to recognise individuals and/or relatives, which might vary under contrasting selection pressures according to social system (Sherbourne *et al.*, 2007), as well as the availability of kin (e.g. in male philopatric species), and by differences in cognitive ability linked to complexity of the social environment (Dunbar, 1998). Other specific, tractable questions warranting further studies relate to the function of female signals, such as copulation calls and sexual swellings, and their role in sexual selection.

VII. CONCLUSIONS

(1) Female mammals regularly compete for access to resources other than mates, including food, nest sites and shelter. Competitive strategies aimed at securing access to resources vary from overt use of

aggression and weaponry, to more subtle behaviours such as threatened or low-level persistent aggression, cooperation, and alliance formation. Notably, female competitive strategies to secure resources, both for themselves and for their descendants, include diverse approaches to inhibiting the reproductive success of rival females and lineages.

(2) Competition for mates may also exert significant selection pressure on female mammals, in some cases leading to the evolution of sexual signals and aggressive competition analogous to sexually selected traits in males. Female mate competition can function to secure access to direct benefits provided by males or to secure future resources by interfering with the reproduction of other females. Moreover, there is growing evidence that sperm may sometimes be a limiting resource for which females compete, due to sperm depletion of competitively successful males.

(3) While important parallels exist between intrasexual competition in males and females, fundamental differences in the reproductive strategies of the sexes often lead to contrasting competitive goals and adaptations. Thus, female adaptations for intrasexual competition are often less conspicuous than those of males, most likely for reasons relating to higher female parental investment and lower potential reproductive rates, and overt displays of female reproductive competition may be less persistently expressed, making them difficult to observe. The reproductive consequences of competition among females are also typically more challenging to quantify, potentially involving effects on offspring quality (survival and reproductive success), inclusive fitness, and on the relative reproductive success of competitors. Hence, although current evidence indicates that variance in the lifetime reproductive success of female mammals can be highly variable in natural populations (in some cases approaching or exceeding similar variation among males), a multigenerational perspective ideally is required to establish the true extent of variation in female fitness which results from intrasexual competition. Consequently, the influence of female competition as an evolutionary selection pressure may have been significantly underestimated to date.

(4) The role of female competition in sexual selection depends on how sexual selection is defined, and assimilating female competition within current definitions is not straightforward because female competition for mates may often function to secure resources utilised for survival (or both survival and reproduction) rather than for reproduction *per se*. With respect to the established definition of sexual selection as arising from differential mating or fertilisation success, our review suggests female competition for the sperm of preferred (or competitively successful) males could be a potentially widespread but previously overlooked evolutionary force. Broader definitions of sexual selection might also be employed to encompass the outcome of female competition for resources other than mates. Although the merits of such definitions are a matter of ongoing debate, our review highlights that understanding the evolutionary causes and consequences of female reproductive competition will require a broader perspective than has traditionally been assumed.

(5) Our review reveals female competition potentially to be a very important selection pressure in the evolution of mammalian reproductive strategies. More detailed investigation is now required to determine the mechanisms and evolutionary consequences of female competition across a broad range of mammalian taxa. Further studies are also needed to identify the long-term consequences of female competition and to determine how social and ecological conditions explain variation in its form and intensity. We conclude that future research in this field offers much exciting potential to advance current understanding of mammalian social and mating system evolution.

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