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Female competition and aggression: interdisciplinary perspectives

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Introduction

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This paper introduces a Theme Issue combining interdisciplinary perspectives in the study of female competition and aggression. Despite a history of being largely overlooked, evidence is now accumulating for the widespread evolutionary significance of female competition. Here, we provide a synthesis of contributions to this Theme Issue on humans and other vertebrates, and highlight directions for future research. Females compete for resources needed to survive and reproduce, and for preferred mates. Although female aggression takes diverse forms, under most circumstances relatively low-risk competitive strategies are favoured, most probably due to constraints of offspring production and care. In social species, dominance relationships and threats of punishment can resolve social conflict without resort to direct aggression, and coalitions or alliances may reduce risk of retaliation. Consistent with these trends, indirect aggression is a low cost but effective form of competition among young women. Costs are also minimized by flexibility in expression of competitive traits, with aggressive behaviour and competitive signalling tailored to social and ecological conditions. Future research on female competition and the proximate mediators of female aggression will be greatly enhanced by opportunities for interdisciplinary exchange, as evidenced by contributions to this Theme Issue.

1. Introduction

Competition to survive and reproduce is fundamental to understanding the biological adaptations of living organisms [1,2]. Within animal populations, competition is often particularly acute among individuals of the same sex because such individuals require the same limited resources to maximize their reproductive success. For example, adult females may require safe nest sites or other limited resources for reproduction [3–8], whereas adult males often compete for mating opportunities with a limited number of sexually receptive females [9,10]. Competition between same-sex individuals, or intrasexual competition, is therefore a widespread evolutionary selection pressure.

Darwin recognized the importance of intrasexual competition, emphasizing 'a struggle between the males for possession of the females' as central to the concept of sexual selection [1, p. 88]. Following Darwin's original insights, much research effort has focused on understanding the mechanisms and evolutionary consequences of reproductive competition among males [10–12]. Adaptations that function in male mating competition include conspicuous traits, such as large body size, weaponry and ritualized displays used in aggressive contests, and diverse showy ornaments or sexual signals used in courtship displays [2,10]. By contrast, understanding of intrasexual competition among females has been slow to develop. Early pioneering work by Hrdy [13], Clutton-Brock [14,15] and others [16–34] highlighted the significance of female–female competition (hereafter, female competition) in diverse animal taxa, including humans. This first tranche of important work, much of which developed in the 1970s and 1980s, provided significant progress in overcoming longstanding female stereotypes within evolutionary biology (see also Hrdy this issue [35]). Nonetheless, research on female competition has taken some decades to develop momentum [6,7,36]. This may be partly due to the inconspicuous nature of competitive interactions

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between females under many circumstances. But perhaps more importantly, it appears that the study of female competition has been constrained by the theoretical paradigms of sexual selection within which most studies of reproductive competition are framed [5–8,13,21,27,36–40]. Emphasis on conspicuous adaptations for mate competition among males has also distracted attention from variation in reproductive success among females. As noted by Hrdy & Williams [37]:

> Sexual selection theory (Darwin 1871, Bateman 1948, Williams 1966, Trivers 1972) is one of the crown jewels of the Darwinian approach . . . Yet so scintillating were some of the revelations offered by the theory, that they tended to outshine the rest of the wreath, and to impede comprehension of the total design; in this instance, the intertwined, sometimes opposing, strategies and counterstrategies of both sexes which together compose the social and reproductive behaviour of a species'. [37, p. 7]

Recent decades have seen revolutionary advances in understanding female roles in sexual selection [41–45], greatly enhancing comprehension of reproductive strategies in both sexes. Notably though, female traits that have been studied most intensively to date, such as mate choice, polyandrous mating and resistance under sexual conflict [11,41–45], each have direct consequences for understanding variation in the mating or fertilization success of males. By contrast, focus on competition-driven variation in female reproductive success has proved more elusive within the field of sexual selection, except in studies of sex role reversed species [5,6,46,47]. Meanwhile, significant advances have emerged from studies of reproductive conflict in social insects and cooperatively breeding vertebrates [48–51], where investigation of female competition is instead built on theoretical foundations of kin selection [52].

Building on these developments in evolutionary biology, a new expansion of interest in female competition is currently underway [5–8,36,40,50,53–80], with ideas increasingly being combined from the complementary research areas of sexual selection and social evolution [50,64]. The aim of this Theme Issue is to further this momentum, driving investigation of female competition beyond recent debates on the terminology of sexual selection [5–8,36,38–40,50] to explore how and why females compete under different conditions, and to investigate the evolutionary significance and proximate mediators of female aggression. Contributions focus on female competition and aggression in humans and other vertebrates, including perspectives from evolutionary biology and game theory, evolutionary, social and developmental psychology, biological anthropology, animal behaviour, neurobiology and endocrinology. By combining ultimate and proximate perspectives from contributors with diverse expertise, our aim is to promote interdisciplinary exchange, thereby generating new synergy and ideas for future research on female competition and sex differences in behaviour. To facilitate such exchange, this introduction offers a synthesis of key issues raised by contributors to the Theme Issue, highlighting areas for future research.

2. Interdisciplinary perspectives on female aggression

(a) Evolutionary perspectives: sex differences and similarities in intrasexual competition

One of the most obvious sex differences in intrasexual competition is that males are typically more overtly aggressive than females. Males are also more likely to have well-developed secondary sexual characteristics, including armaments and ornaments, for use in direct contests and competitive signalling [2,5,10]. These common sex differences can be explained with reference to post-Darwinian sexual selection theory. Males are typically regarded as the more competitive sex in the context of sexual selection because they usually have lower potential reproductive rates than females (defined as the maximum number of independent offspring that can be produced per unit time) [81,82]. This means that at any given time fewer females than males will be ready to mate, and males will be selected to compete for mating opportunities. Although sexual selection theory offers a powerful explanation for sex differences in competitive behaviour [83], examples of intense female competition and aggression are not uncommon across a wide range of species with conventional sex roles [5–7,13,36]. In exceptional cases, adult females of certain species are consistently more aggressive than males [5,7,84]. More generally, females can occasionally be as aggressive as males (or more so) in competitive interactions [5,7,50,65,84–87]. Hence an important goal is to determine how and why the competitive responses of the sexes are similar or different under various conditions, including competition for resources as well as mates.

As highlighted in this Theme Issue by Clutton-Brock & Huchard [80], there are many qualitative similarities in intrasexual competition between males and females, as exemplified by instances of competition for resources needed for survival and reproduction among social or group-living species (see also [3,4,79]). For both sexes, living in groups intensifies competition for limited resources, such that selection favours traits that enhance competitive ability. Similar competitive traits, including displays and ornaments, as well as weaponry and aggression, are found in both sexes to varying degrees, and competition for resources is mediated by social mechanisms that operate both within and between groups. Moreover, the selection pressures responsible for the evolution of competitive traits in females often appear similar to those in males, including intrasexual competition for breeding opportunities and to attract preferred mates [5–7,36,79,80].

The greater investment usually made by females in producing and rearing young is likely to be an important factor underlying sex differences in competitive strategies [5–7,56]. For example, trade-offs with offspring production may constrain female investment in costly competitive signals [88,89]. For both signalling and aggression (see also §2b), flexibility of expression may therefore be particularly beneficial for females, allowing competitive effort to be optimized according to social conditions. Such flexibility is illustrated by plasticity in the expression of odour signals and scent marking behaviour of female mammals, as described by Stockley *et al.* [90]. Under non-competitive conditions, female house mice (*Mus musculus domesticus*) have a much lower concentration of protein in their urine compared to males, reflecting lower investment in the production of major urinary proteins (MUPs) used in scent communication. Plasticity in MUP production according to the social environment is found in both sexes, but the increase in female urinary protein content under competitive conditions is particularly dramatic and is correlated with aggressive behaviour of female mice. Plasticity in expression of costly competitive signalling thus allows females to tailor energetic investment according to local conditions and likely reproductive benefits. Similarly, as discussed in §2b, the expression of aggressive behaviour by females is typically variable, with average levels well below those of males, and escalated aggression reserved only for the most intense competitive situations yielding high reproductive reward or defence of offspring.

Competition for breeding opportunities can be particularly intense in singular cooperative breeding vertebrates, where reproduction within social groups is largely monopolized by a single dominant female. Under such conditions, variance in the number of offspring produced by females may exceed that among males [50], a reversal of the more usual pattern invoked to explain male-biased sexual dimorphism in body size, ornaments and armaments. In species with particularly extreme reproductive skew among females, the usual patterns of male-biased sexual dimorphism in competitive traits might therefore be reversed. That is, females might be predicted to be the larger or more heavily armed sex, owing to more intense selection to win in contests for reproductive opportunities. The contribution by Young & Bennett [91] explores this idea using data from cooperatively breeding Damaraland mole rats (*Fukomys damarensis*). As in many other cooperative breeders, competition for reproductive opportunities is particularly intense in this species, and variance in reproductive success appears to be higher among females than males. Nonetheless, males are still the larger and more heavily armed sex, a pattern that is repeated in other cooperatively breeding vertebrates. Young & Bennett [90] propose two potentially general evolutionary mechanisms to explain why competitive traits are typically less exaggerated among females than males in cooperatively breeding mammals and birds, despite females often showing higher reproductive variance. Firstly, fundamental differences in the reproductive biology of the sexes, such as higher costs of reproduction among females, could leave reproductive conflict among females more readily resolved to restraint among subordinates rather than escalated physical contests with their dominant. Secondly, sex differences in the incidence of competition with relatives in the kin-structured societies of cooperative vertebrates may frequently leave the relative variance in reproductive success of the sexes a poor proxy for the relative variance in inclusive fitness. Wherever sex differences in the spatial scale of competition or patterns of dispersal leave females competing more frequently with kin, this may differentially relax the variance in inclusive fitness arising from intrasexual competition among females, tempering the exaggeration of competitive traits. Indeed, these mechanisms could play a more widespread role in the outcomes of intrasexual selection than is currently appreciated, as sex differences in reproductive biology, dispersal and kin structure are pervasive across non-cooperative taxa too.

Patterns of dispersal in human societies are variable and linked to reproductive conflict among females [61,74,75]. As reported in the current issue by Ji *et al.* [92], the Mosuo of southwestern China are unusual in that neither sex disperses. Instead, brothers and sisters of three generations live together in communal households with matrilineal offspring, and men visit their wives only at night in ‘visiting’ marriages. Reproductive competition between sisters may therefore result from sharing resources, and Ji *et al*. [92] provide evidence that the reproductive success of Mosou females is negatively influenced by co-resident female kin (see also [93]), with the presence of sisters associated with significantly suppressed fertility and later age at first birth. Consistent with predictions of a ‘tug of war’ model of reproductive skew, older Mosuo sisters appear to win the conflict and have more offspring than their younger sisters, but they also put more effort into communal farming that supports all the family. As with studies of cooperative breeding in other species [91], this work underlines how competition for shared resources can significantly impact female reproductive success even when competitors are close relatives, although understanding the resolution of such conflict requires careful consideration of inclusive fitness consequences.

In contrast with the Mosuo, females in many other human societies transfer from their natal family group at marriage, and are thus more likely to encounter competition with non-relatives [61,74,75]. This pattern of female transfer contrasts with the male-biased dispersal more typical of other mammals. However, Pusey & Schroepfer-Walker [86] in the current issue note that female-biased dispersal is also found in chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*), as well as in many human societies, suggesting a pattern of male philopatry and female dispersal as the shared ancestral condition for this lineage. Hence during human evolution, females would often have been competing with non-relatives for essential resources required to survive and reproduce, perhaps ultimately favouring the formation of strong stable bonds and coalitionary relationships between unrelated females.

(b) Behavioural perspectives: how do females compete?

Diverse behavioural strategies have evolved under intrasexual competition in both sexes, with aggression expressed in a variety of forms. At one extreme, aggression can be direct and unrestrained, with combatants engaged in escalated contests likely to cause serious injury or death. Such extreme aggression is rare in animal societies and is usually associated with situations where the stakes of winning are unusually high, such as when males compete for exclusive mating access to a large number of females [15]. Notably though, examples of lethal aggression are occasionally reported for females in competition for resources essential for reproduction [60,86,94–97]. More typically, injurious aggression is avoided [98]. In species with stable social relationships, competitive interactions can be managed within dominance hierarchies without the need for repeated direct aggressive contests, and dominance status is often linked to reproductive success in both sexes [7,15,76]. Escalation of aggression may also be avoided by settling contests via ritualized displays or signals that reveal asymmetries in the competitive ability of opponents [99,100]. Notably though, it has been argued that females of some species may be less likely than males to engage in ritualized displays, and more likely to engage in high-risk fighting tactics leading to injury or death in direct contests for particularly valuable resources [36,97]. More commonly, competitive interactions may often be so subtle as to go unnoticed in behavioural observations, with conflict resolution based on threats and indirect aggression rather than direct combat (see contributions to this issue by Pusey & Schroepfer-Walker [86], Benenson [101], Campbell [102], Cant & Young [103] and Vaillancourt [104]). As discussed below, female competitive interactions include a broad repertoire of aggressive strategies, tailored to social conditions at both population and individual levels.

The diversity of behavioural strategies used by females in the context of resource competition is illustrated by long-term field studies of chimpanzees described by Pusey & Schroepfer-Walker [86]. The reproductive success of female chimpanzees depends critically on sustained access to high-quality food resources. Dominant females win direct contests for food and gain preferential access to preferred foraging sites. Dominance rank is therefore correlated with reproductive success. Direct aggression is usually avoided by females foraging alone or in small groups within distinct but overlapping core feeding areas. However, heightened and sometimes severe aggression can be directed towards immigrant females, and infanticide by females of newborn infants of community members is not uncommon. In each case, the intensity of aggression is correlated with population density, and aggressive behaviour can be interpreted as a strategy to reduce competition for space and resources. Aggressive behaviour often involves 'ganging up' by females or coalitionary attacks, presumably to minimize risk of retaliation or injury. Female chimpanzees therefore appear to employ intense aggression on occasions where high benefits, in the form of reduced future competition, can be achieved at relatively low cost.

Women are more sociable than female chimpanzees and their closer mutual proximity creates scope for frequent conflicts of interest and competition. Yet, like female chimpanzees, women display considerably less physical aggression than their male counterparts. For the most part, young women's competition is, directly or indirectly, about men and the resources they can provide. Hence it is perhaps unsurprising that women compete about those qualities that are highly valued by men: youth and attractiveness. Men find dominance or status less attractive in a prospective mate than do women [105], which may contribute to women's less overt striving for rank. When competition escalates in intensity, it typically involves the use of indirect aggression such as reputational attack, stigmatization and exclusion (see contributions to this issue from Benenson [101], Campbell [102] and Vaillancourt [104]).

Women in Western societies typically restrict their competition to epigamic display and indirect aggression, but Campbell [102] describes how ecological factors in inner city areas may conspire to escalate levels of competition to physical confrontations. Levels of endemic poverty combined with an unfavourable sex ratio and high variance in male income puts a premium on well-resourced men, increasing competition for even short-lived relationships with them. In such neighbourhoods, young women sometimes employ coalitionary aggression against 'immigrant' females who threaten local resources. Aware of men's taste for novelty, gang girls are extremely sensitive to the arrival of new girls in the neighbourhood [106]. This can lead to group-level attacks on girls they perceive as 'stealing' their men. Female newcomers seeking entry to the gang are also treated with suspicion: to prove that they are not merely seeking access to the male members, they must be 'jumped in' (required to fight with an established female member).

Although female competitive strategies are diverse across different species, in many cases they need not involve conspicuous aggression. For example, where food resources are widely dispersed or difficult to monopolize, scramble competition may prevail with little direct interference [107]. Conflicts over reproduction in social species also often appear to be resolved without overt aggression, and Cant & Young [103] explore potential behavioural mechanisms by which this might be achieved. Recent theoretical models investigate the use of threats as a behavioural mechanism that animals can use to control one another's behaviour. Consider a situation where both a dominant and subordinate female require the same limited resources to reproduce. If the subordinate female attempts to take more resources than the dominant is willing to tolerate, the dominant female may respond by aggressively evicting the subordinate from the group, or killing any offspring that she is able to produce. Under such circumstances where dominant females are capable of effectively disrupting or punishing subordinate reproduction, the threat of such direct aggression may be sufficient to deter a subordinate from attempting to reproduce, particularly where the cost of a failed reproductive attempt is high. Reproductive conflict will thus be resolved without the expression of overt aggression, since where a threat is effective it will rarely need to be carried out. Importantly, Cant & Young [103] conclude that compared to males, conflict among females will often be settled by such covert threats of punishment, rather than overt acts of punishment.

In considering theoretical approaches to peaceful conflict resolution among females, Cant & Young [103] contrast 'sealed bid' models with sequential models of punishment. The latter, in which strategic decision-making is contingent on another's behaviour, clearly fits with the 'social brain' and interpersonal skills of our own species. Among men, dominance is often situationally negotiated with threat playing a key role. Studies of the dyadic sequencing of naturally occurring aggressive encounters between men show that there is a predictable series of events that begins with a verbal attack by actor A on B's social standing or credibility. To avoid losing 'face', B demands that the slight be withdrawn. If A refuses, there is a contingent threat of escalation by B, which terminates in either A's withdrawal or a mutual agreement to fight [108]. Escalated physical conflicts of this kind between women are rarer. This is not to say that women do not seek to exert control over others' behaviour, but typically girls learn to achieve this in subtle ways designed to avoid direct confrontation [101]. Girls, who fail to adjust their behaviour in response to these covert 'requests', can be (subtly) threatened with friendship withdrawal and social exclusion.

The implementation of punishment in animal societies, such as eviction of competitors from the social group, can involve significant costs for females [109,110]. By contrast, women's use of social exclusion (rather than outright physical aggression) provides an effective form of punishment with minimal energetic expenditure or risk of physical injury [101,102,104]. Rather than inflicting costly punishment, deviants can be effectively controlled by indirect means such as refusal to cooperate with them, destruction of their reputation (so that others will also refuse cooperation) and, ultimately, exclusion from the group. Indirect aggression (the use of pejorative gossip and social exclusion) is women's preferred aggressive tactic. Because harm is delivered circuitously and because it is executed simultaneously by several members of the community, it is a low-risk strategy. Benenson [101], Vaillancourt [104] and Campbell [102] explore the advantages of such indirect forms of aggression for women. The strong bonds between women and their emotional interdependence make victimization by indirect aggression a particularly painful experience, leading to depression and even suicide [101].

Cant & Young [103] also note that, in the context of sequential models of punishment, reduced asymmetry between individuals in the power to punish is likely to increase the advantages of social sensitivity to another's behaviour. In women, a strong norm of egalitarianism reduces manifest power differentials and women are highly sensitive to threats of rejection. They are more susceptible to group pressure than men [111]; their self-worth is more strongly dependent on peer evaluations [112], and they are more punishment sensitive [113]. Women also exceed men in the ability to decode emotional signals from visual and aural information [114] and perform better in tests of mind-reading and empathy [115]. These enhanced social skills may allow women to detect subtle forms of threat and avert direct conflict.

(c) Proximate perspectives: mediators of female aggression

Contributors to this Theme Issue explore several proximate mediators of female aggression, including hormonal, neurobiological and cultural influences, which facilitate flexible responses to rapidly changing social environments.

French *et al.* [84] explore hormonal mediators of female aggression among 'atypical' mammals in which females are more aggressive than and/or are dominant to males, including the role of androgenic steroids in both the developmental organization of neural structures underlying aggression [116], and the activation or facilitation of aggressive behaviour [117,118]. Both sexes produce testosterone (T) in the brain and gonads, possess androgen receptors in neural and peripheral tissues, and show behavioural and physiological responses to T [119]. From a developmental perspective, effects of prenatal T exposure can facilitate aggression in later life [120], although French *et al.* [84] present contrasting findings for mammals with high female aggressiveness. Such diversity reveals that our understanding of the role of prenatal androgen exposure in mediating female aggression is still far from complete. In adulthood, female T levels are typically lower than males, even in species where females dominate males or are unusually aggressive ([84]; see also Rosvall [121] and Campbell [102] this issue). This suggests that T level alone is unlikely to fully explain sex differences in aggression. Interesting though, levels of the T precursor androstenedione (A_4) are more comparable between the sexes in certain female-dominant species, such as spotted hyenas (*Crocuta crocuta*) and ring-tailed lemurs (*Lemur catta*) [84]. Studies of brain structure in adult spotted hyenas also reveal evidence of reduced sexual dimorphism in parts of the hypothalamus involved in mediating male-typical behaviour in mammals, hinting at neural substrates for enhanced female aggression [122]. Clearly, there is much still to learn regarding hormonal mediators of female aggression, and the contribution by French *et al.* [84] highlights that the diversity of evolved mechanisms in non-model organisms can provide insights of comparable significance to genetic manipulation of more conventional laboratory models.

T appears to mediate female aggression to some extent in more typical vertebrate species also [121], and since females with elevated T levels are likely to incur reproductive costs such as decreased fertility or maternal care of offspring, the physiological mechanisms by which aggression is mediated to minimize associated costs are also of interest from an evolutionary perspective [84,121]. To minimize reproductive costs, females need a way of directing T to only those processes and behaviours where it offers benefits [121]. This might be achieved by reducing T sensitivity in some tissues (such as neural sites associated with maternal care), while increasing sensitivity in others (those involved in competition). One route to sex-specific effects of T examined by Rosvall in the current issue [121] is differential gene expression. Experimental elevation of T in dark-eyed juncos (*Junco hyemalis*) affected the expression (transcription) of genes in the medial amygdala and hypothalamus, areas of the brain linked with aggressive and social behaviours. The affected genes included those known to mediate aggression, notably aromatase and monoamine oxidase A [123]. Importantly, males and females overlapped in less than 1% of genes affected by T treatment, suggestive of sex-specific genomic responses to T. There is also intriguing evidence that gene networks (genes whose expression are correlated) are more modular in females and this may allow females to regulate parcels of genes in a modular fashion [124]. Hence this may allow females greater flexibility to express aggressive behaviour while still maintaining normal fertility and parental behaviour [121].

A peptide hormone that has sparked an explosion of research in recent years is oxytocin (OXT). In addition to its peripheral effects on childbirth and lactation, it has central effects on regions identified as part of the social brain network [125]. OXT has been implicated in a range of prosocial and some antisocial human behaviours [126,127]. Dubbed the 'tend-and-defend' effect, OXT enhances a sense of in-group identity and favouritism but also fosters antagonism and defensive aggression towards threatening out-group rivals [128]. This double-sided effect gels well with our understanding of the role of OXT in maternal care and aggression [85]. The challenge has been to identify how OXT can facilitate both attachment to offspring and hostility to those who threaten them. In this issue, Bosch [85] suggests that the answer lies with a reduction in state anxiety. Bosch and co-workers bred rat lines (*Rattus norvegicus*) for high and low anxiety with interesting results. High anxiety mothers show more attentive maternal behaviours and more frequent attacks on intruders, with shorter latencies and higher overall aggression. This aggressive reaction appears to stem from their acute OXT response to threat in the paraventricular nucleus of the hypothalamus and central amygdala. However, the sister nonapeptide of OXT, arginine vasopressin (AVP), is also influenced by selective breeding of rats in these studies. Early evidence suggests that AVP release is also positively associated with maternal aggression, although OXT and AVP appear to have antagonistic effects. Importantly, both OXT and AVP are also modulators of anxiety, although the complex interacting effects of these neuropeptides remain to be understood. As discussed by Campbell in this issue [102], fear modulation holds a central place in explaining aggression more generally and the anxiolytic effects of OXT make it a strong candidate mechanism. Campbell [102] argues that, at a proximate level, the evolved emotions of fear (avoidance) and anger (approach) are relevant to the decision to engage in physical aggression. While sex differences are not found for anger, they are consistently present for fear, and women's higher levels of fear may be an adaptation to ensure their survival on which their children's lives depend.

In humans, a further species-specific mediating factor is the socialization of girls into cultural expectations about sex-appropriate behaviour. In addition to shaping greater desistance from direct aggression, cultural values also influence women's avoidance of advertising superior rank. The result is a flatter dominance hierarchy and greater egalitarianism [129,130]. Women are also more likely than men to use affiliative speech styles and less likely to use assertive styles [131,132]. As discussed by Benenson [101] in this issue, these sex differences become manifest early in the preschool years at the same time as sex-segregated peer groups emerge. The tendency to prefer same-sex playmates is universal and sets the scene for close peer scrutiny of sex-appropriate behaviour. 'Gender-streaming' of social information is enhanced by sex segregation which both increases the differences between boys' and girls' groups and minimizes variability within each group. Boys and men spontaneously form dominance hierarchies and value competitive games, whereas girls and women enforce a strong egalitarian norm based on interdependence and the eschewing of manifest power differentials [101,133]. For the majority of adolescent girls, competition is restricted to forms of mate attraction: vying to attract male attention while avoiding the appearance of hubris or sexual availability [102,104]. In settings where mate competition is more intense, such as inner city areas where men are in short supply and where male variance in resources is marked, cultural norms are adjusted to tolerate (and sometimes applaud) direct forms of female aggression (see Campbell [102] this issue). In these settings, girls do not view themselves as 'unfeminine' because stereotypes about what constitutes femininity are adjusted to accommodate the exigencies of their situation.

3. Directions for future research: broadening horizons in the study of female competition

As highlighted by contributions to this Theme Issue, the study of female competition is advancing rapidly with much potential for interdisciplinary exchange. Below we summarize some significant future challenges emerging from the studies presented (see also [7,36]).

Identifying phenotypic traits linked to variation in reproductive success is fundamental to understanding adaptations to intrasexual competition [134]. A focus on social species has produced striking data on reproductive skew among females of cooperatively breeding vertebrates, as a stimulus for further theoretical and empirical investigation [50,51,91]. However, variation in female reproductive success is less well understood in other species [7,15,76]. For a broad ecological perspective, data are needed across diverse animal taxa, including social, pair-living and solitary species with contrasting life histories. Because females often invest in offspring quality as well as numbers, it is also important to consider variation in the reproductive success of their offspring as well as the number successfully reared to independence. This is increasingly achievable in the context of long-term datasets collected under natural conditions, as well as controlled experimental studies.

Constraints on female competitive traits are a recurring theme in contributions to the current issue. Costs of reproduction may constrain overall investment by females in competition, influence the form that competition takes, or affect the physiological and psychological mechanisms underlying competition. Trade-offs with offspring production or parental care are commonly invoked as potential constraints on female investment in costly competitive behaviour, weaponry or signals [88,89,135]. However, empirical support for this idea is currently limited and offers mixed results [109,110,136–138]. Further empirical tests are needed to quantify the short-term reproductive costs of female competitive investment, which may also vary according to dominance status, age or condition [63,109,110]. Over evolutionary timescales, high costs of reproduction may predispose females to exercise reproductive restraint rather than compete directly for reproductive opportunities, with consequences for understanding sexual dimorphism in body size and weaponry among cooperatively breeding vertebrates [91]. More generally, high costs of reproduction are associated with a variety of physiological mechanisms that allow investment in rearing offspring to be postponed under unfavourable or stressful conditions [139,140]. Such mechanisms can be exploited to inhibit the reproduction of competitors and could be a potentially widespread source of variation in female reproductive success [57,139,141,142].

As is clear from several contributions to the current issue [80–85,86,90,121], females may often invest flexibly in competitive effort according to immediate need. Hence aggression may be heightened at specific reproductive or life-history stages when competition for mates, resources or the need to defend offspring is particularly acute [57,68,85,102,109,110,143]. By extension of this general pattern, Pusey & Schroepfer-Walker [86] note that establishing high social rank is particularly important for female chimpanzees when they transfer between social groups and suggest it would be of interest to determine whether females of transfer age in species with female-biased dispersal experience underlying hormonal changes that may enhance their aggressiveness. The potential for similar context-specific investment in heightened aggression could also be explored in other species, including humans, according to social and ecological conditions. From a proximate perspective, understanding the underlying mechanisms by which flexibility in aggressive behaviour is mediated is also an important goal. Here, as highlighted by Rosvall [121] and French *et al.* [84], a broad comparative approach is ideally required to explore the evolution of hormonal and genetic mechanisms that allow females to maximize the benefits of aggression, while minimizing the costs.

Evidence from long-term field studies of chimpanzees also reveals that the frequency and intensity of female aggression varies according to competitive pressure at a population level [86]. Long-term data such as these are still rare but provide valuable insights into evolutionary and ecological conditions promoting escalated aggression in the context of intense resource competition. Similar effects can also be seen over much shorter timescales in experimental studies of house mice, where adult females dramatically increase investment in competitive signalling, linked to aggression, under competitive conditions [90]. These findings highlight plasticity of behaviour in response to population-level competitive pressure as a useful focus for future investigation. From a proximate perspective, French *et al.* [84] also note that more studies are needed to explore plasticity in the androgen levels of adult females as a consequence of rates of agonistic interactions (see also [144]).

The social environment can also have significant consequences for the development of behavioural phenotypes, and competitive behaviour may be tailored adaptively according to prevailing social conditions experienced during pre- and postnatal development or adolescence [145,146]. Adverse early life experience may trigger developmental responses that are potentially adaptive in human adulthood too, such as greater risk taking behaviour, heightened aggression or early reproduction [147,148]. Hence there is much potential for future investigation of how early experience influences the development of female behaviour and life-history traits as an adaptive response to social competition. Also in humans, much remains to be learned about how cultural values concerning 'appropriate' forms of female competition are shaped by local ecological demands.

Variation between individuals in response to competitive conditions is also worthy of more detailed investigation. Why, for example, might some females within a population choose to delay reproductive maturation or suppress their own reproduction in response to a competitive threat, whereas others instead increase competitive effort? In addition to developmental influences mentioned above, links between competitive behaviour and behavioural syndromes or personality traits might offer new insights into individual variation in humans and other species [149–151]. In humans, one approach widely employed by psychologists emphasizes differences in punishment and reward sensitivity, which are argued to underlie individual and sex differences in personality [151–153]. This approach could be used to explore individual variation in status motivation, since power yields resource abundance and the achievement of power depends on an acutely sensitive reward system combined with hyposensitivity to punishment [154]. Functional individual variation in hormones is also of relevance, but is still a relatively neglected area of investigation [155]. Here, there is potential to explore mechanisms underlying individual variation in female behaviour and reproductive suppression, for example, involving gonadotropin inhibitory hormone (GnIH), which suppresses the hypothalamic-pituitary-gonadal axis and is responsive to stress and environmental cues in vertebrates [156,157].

Fitness consequences of female competition are often related to resource acquisition [7,76,86]. However, competitive outcomes among females may also have significant fitness consequences via resultant paternity of offspring. As reported in this issue, female house mice investing heavily in odour signals related to competitive ability appear more likely to mate with high-quality males and produce offspring by fewer different sires [90]. By contrast, evidence for social lizards (*Egernia whitii*) indicates that the most aggressive females are more likely to produce offspring sired by multiple males [158]. In both cases, individual variation in female competitive behaviour is likely to have important long-term fitness consequences via modes of paternity acquisition, although the quantification of such benefits and understanding their wider significance across taxa remains an important future challenge.

Several contributions to this Theme Issue highlight the need to better understand how females compete, and the differences and similarities in intrasexual competition between females and males [80,90,91,103]. Cant & Young [103] emphasize that covert threats of punishment may more often lead to peaceful resolution of social conflict between females compared to males, with lower probabilities of direct aggression. Clearly, creative experimental approaches are needed to test burgeoning theory in this field. It has also been suggested that direct fights between females might follow different rules than those between males, with female aggression potentially more dangerous under certain conditions [36,97]. Further investigation is needed to explore this idea, which might also potentially apply in humans. Because physical fights between young women are rare, we have few descriptions of what actually takes place. Weapon use is rare which limits potential injury and there is a taboo against 'fighting like a girl' (spitting, scratching, pulling hair), which suggests that tactics are subject to social norms. However, girls' fights are often reported to be 'wilder' than those of boys; more emotionally and behaviourally unconstrained [159,160]. While men view their aggression as a means of imposing control over others' misbehaviour, women view their aggression as a loss of inhibitory control resulting from very high levels of anger [161]. Unlike boys, girls may not be socialized during childhood into the social rules that govern the conduct of 'fair' fighting. Ethnographic descriptions of fight behaviours, as well as their rhetorical presentation, are needed.

Significant gaps also remain in our understanding of the functions and fitness consequences of female competitive signals. Most interest to date has focused on female visual signals and ornamentation [40,55,56,64,162–165]. However, odour and vocal signals are likely to play a significant role in the competitive interactions of females in many species but remain relatively neglected by comparison [90,166–168]. In each case, empirical studies are needed in a broad range of taxa to explore if signals are aimed at other females, potential mates or both, and to determine what information is being conveyed [169]. It is also important to explore how competitive signalling translates into variation in reproductive success among females via access to resources needed to reproduce and/or male mate choice. In humans, traits advertised by women and preferred by men are relatively well studied [105]. But in other species, it is often unclear if male attraction to particular signals is based on female fertility or receptivity (i.e. immediate reproductive opportunity), fecundity and/or some other form of female quality such as ability to monopolize key resources [90].

Finally, it is increasingly clear that intrasexual competition is intricately linked to social behaviour. Compared to direct forms of aggression observed in other species, the use of social exclusion by human females is a relatively low-cost strategy and is typically associated with coalitionary and egalitarian behaviour. This is of particular relevance to the study of human social evolution, as low-cost punishment strategies are hypothesized to deter 'free-riders' and allow cooperation to be sustained in social dilemma games [170,171]. A focus on social or group-living species also offers exciting possibilities to explore fitness benefits of coalitions and the evolution of cooperative behaviour under competitive scenarios within and between social groups [20,172–175].

As evidenced by the contributions that follow, there is much to be gained from reciprocal exchange of ideas between researchers studying humans and other species. Although the study of female competition has been slow to develop, its broad evolutionary significance is now clear. Further advances in understanding female adaptations to intrasexual competition and the proximate mediators of female aggression will be greatly enhanced by opportunities for interdisciplinary exchange.

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