Research

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Sex bias in intergroup conflict and collective movements among social mammals: male warriors and female guides

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Intergroup conflict is a major evolutionary force shaping animal and human societies. Males and females should, on average, experience different costs and benefits for participating in collective action. Specifically, among mammals, male fitness is generally limited by access to mates whereas females are limited by access to food and safety. Here we analyse sex biases among 72 species of group-living mammals in two contexts: intergroup conflict and collective movements. Our comparative phylogenetic analyses show that the modal mammalian pattern is male-biased participation in intergroup conflict and female-biased leadership in collective movements. However, the probability of male-biased participation in intergroup conflicts decreased and female-biased participation increased with female-biased leadership in movements. Thus, female-biased participation in intergroup conflict only emerged in species with female-biased leadership in collective movements, such as in spotted hyenas and some lemurs. Sex differences are probably attributable to costs and benefits of participating in collective movements (e.g. towards food, water, safety) and intergroup conflict (e.g. access to mates or resources, risk of injury). Our comparative review offers new insights into the factors shaping sex bias in leadership across social mammals and is consistent with the 'male warrior hypothesis' which posits evolved sex differences in human intergroup psychology.

This article is part of the theme issue 'Intergroup conflict across taxa'.

1. Introduction

A striking, yet often overlooked feature of human intergroup violence is a massive gender bias in participation. Whenever humans form coalitions to injure or kill members of other such coalitions, they virtually always consist exclusively of men. Warfare among human hunter-gatherers is exclusively a male affair [1]. All historical armies lacked female members, and a strong male bias can be found among contemporary urban gangs and terrorist groups [2,3]. Only the last decades have seen deviations from this pattern, such that some contemporary armies have obligatory conscription for women (e.g. Israel, Norway), but women remain excluded from front-line combat units in all but 17 countries [4]. Looking at war across human history and cultures, it is, therefore, justified to view warfare as 'a strategy by which *coalitions of*

males (our emphasis) cooperate to acquire and defend resources necessary for reproduction' [5, p. 963]. Even though warfare may have shaped key aspects of human psychology [6,7], including fundamental gender differences in social psychology [8], the underlying evolutionary origins of this gender bias in participation in intergroup violence has always been taken for granted, and comparative perspectives have rarely extended beyond chimpanzees [5,6]. Here, we offer a broader comparative perspective that examines the nature and potential drivers of sex biases in participation in intergroup conflict across diverse mammalian societies [9].

Intergroup conflict is also a major evolutionary force shaping animal societies [10–12], with the benefits of joint resource defence arguably favouring the formation of permanent social groups, as well as increased tolerance and cooperation within these groups [13–15]. However, collective intergroup aggression also poses a collective action problem: why should an individual risk being killed or injured in territorial defence when it could still reap the benefits without incurring the costs of producing them? Despite these risks [16,17], selection may favour intergroup conflicts when members of winning groups gain increased access to contested resources [14,18], such as territories and mating opportunities [19,20]. Evolutionary game theory also predicts that variation in the fitness consequences of fighting should be an important determinant of which individuals participate in fights [21]. In the extreme case when conflicts are potentially fatal, individuals are expected to participate over contested resources only when the resource value exceeds that of living into the future [22]. In some cases, the costs of losing and benefits of winning such resources are evenly distributed across group members [23,24]. In other cases, the associated costs and benefits of participation in intergroup conflicts are not equally shared among individuals [25–29]. For example, in groups with steep dominance hierarchies, high-ranking individuals may gain more benefits from intergroup conflict compared to low-ranking individuals because they have priority of access to resources [26,29–37], but this gain may be partly offset by the greater effort expended during intergroup conflicts [18]. Similar asymmetries are expected when individuals differ in motivation, strength or costs incurred [18].

The balance of the costs and benefits of participating in collective action in general, and potentially lethal intergroup conflict in particular, are also expected to vary, on average, for males and females. Because female reproduction in mammals is constrained by the energetic demands of gestation and lactation, female fitness is primarily limited by access to food and caring for young [38–40], and we might, therefore, expect females to be more involved than males in managing collective movements to locate food or safety to support their current and future reproduction [39,41,42]. Increased access to food gained from winning intergroup conflicts, however, is generally unlikely to overwhelm the risk of injury or death for females or their offspring, particularly since female fitness increases throughout the reproductive lifespan. However, females may engage in intergroup conflicts when the costs of engagement are similar for both sexes, or in female-dominated societies in which females have priority of access to defensible food resources over males (e.g. ungulate prey for spotted hyenas [30]). Moreover, in cases where highly valuable food, water or shelter is defensible, females may also incentivize male participation in intergroup conflict [43,44] to secure access to these resources.

Males, on the other hand, primarily compete for access to fertile females, which generally represent a more limited and less divisible resource than food [38–40]. Moreover, the evolutionary fitness of defence of current reproductive opportunities (mates) is expected to exceed their future reproductive value more often for males than for females owing to limited role of paternal care in most mammals. As a result, males in many species are subject to stronger intrasexual competition and have evolved traits that help them monopolize females and gain mating opportunities [32,37,45,46].

Game theory further predicts that the probability of winning conflicts and the likelihood for an individual to reap the benefits from winning should increase with the relative body (e.g. a large male versus a small female) and weapon size of an individual compared that of other contestant(s) in a fight [21]. Thus, male-biased participation in intergroup conflicts may be particularly strong when sexual size dimorphism is pronounced, a trait that often covaries with weaponry, most prominently with canine size dimorphism in primates [47–49]. Given that females are food limited, participation in intergroup conflicts by both sexes may be more equitable for mammals that feed on highly defensible food, such that both males and females may benefit from their defence (e.g. females gain access to contested food, males defend food to attract females). Thus, we expect sexual dimorphism and resource defensibility to be key predictors of sex-biased participation in intergroup conflict.

Despite these theoretical considerations, evidence for sex differences in intergroup conflict is mixed. A recent meta-analysis found moderate sex differences in intergroup aggression among primates but this was not statistically significant after correcting for evolutionary history [36]. In some primates, such as bonnet macaques (*Macaca radiata*) [32] or black and white colobus (*Colobus guereza*) [50], males tend to be more aggressive than females during intergroup conflicts [23]. In other primates, such as Verreaux's sifakas (*Propithecus verreauxi*) [51] and Samango monkeys (*Cercopithecus mitis erythrarchus*) [45], females are equally or more aggressive than males. Moreover, in vervet monkeys (*Chlorocebus pygerythrus*), females initiate intergroup conflicts because doing so provides them with immediate access to limited food; in these groups, females harass low-ranking males to participate in intergroup conflicts [44,52]. Thus, sex differences in behaviour during intergroup conflict may not generalize across primates [36] and such differences have yet to be quantified across social mammals more generally.

Our aim was to investigate sex-biased participation in intergroup conflict and sex-biased leadership in collective movements across mammals, controlling for phylogeny. Given the considerations about differential incentives above, we also tested whether sexual size dimorphism and food defensibility predict sex bias and whether primates differ from non-primates since most primate females carry their infants which poses an additional cost to female participation in intergroup conflict [41]. Importantly, both contexts (intergroup conflict and collective movement) require coordination among multiple group members [36,53–55] and the evolution of sex-biased influence in one context may, therefore, facilitate it in the other; hence we also tested whether sex bias in collective movements predicted sex bias in intergroup conflict. Biased influence by some individuals on the decision-making

process is commonly referred to as leadership in the context of collective movements (also called group travel) [56–58]. As we discuss in the next section, while some have extended the leadership concept to explain patterns of collective action during intergroup conflicts [59,60], it is much less studied in this context.

2. Methods

(a) Operational definitions for comparisons of sex differences in collective action

In the collective movement context, we recorded sex-bias in leadership. Leaders are generally defined as individuals that have a disproportional influence on collective behaviours of a group, regardless of how influence is achieved [49,51,61]. In the context of collective movements, we operationalized leaders as individuals that successfully initiate group movements, that is, those that move first in a direction and disproportionally influence other group members (e.g. by recruiting followers). Importantly, leadership is distinct from dominance; the latter is defined as the ability to win dyadic fights and results in priority of access to resources whereas the former focuses on influence in a decision-making hierarchy [62,63]. In the context of group movements, leadership is rarely based only upon physical force [58] but rather on followership (e.g. ability to recruit followers) [64,65]. In some cases, high-ranking individuals also lead [66,67] but leadership in animals aligns more closely with the concepts of power in sociology [68] and prestige (or status) in psychology [69,70].

Within the context of intergroup conflicts, we were limited to quantifying sex bias in participation (see also [36]). Although influential individuals are often the ones at the front lines of intergroup encounters and those that direct significantly more aggression towards individuals from other groups, intergroup conflicts involving multiple individuals joining forces are often difficult to track, particularly for primate groups with large numbers of participants or occurring within forests with low visibility in three-dimensional space; hence we could not consistently record leadership.

(b) Literature search and data collection

Our current study builds on recent reviews of collective decisions in group-living mammals [29,60,71–73], papers citing these reviews, and other papers identified via Google Scholar searches to identify species that engage in collective action during intergroup conflict, movements or both. We focused on species living in mixed-sex groups, excluding those for which adults are sexually segregated [74,75]. This yielded studies for 72 species (see figure 1) that spanned five biological orders within the Class *Mammalia*, including *Artiodactyla* (three species of even-toed ungulates), *Cetacea* (four species of whales and dolphins), *Carnivora* (10 species of carnivorans), *Perissodactyla* (two species of odd-toed ungulates) and *Primata* (53 species of primates). We scored each species and context as female-biased, no sex bias (sex differences not statistically significant), or male-biased (figure 1; electronic supplementary material, table S1) based on the analyses presented in the original studies. Sexual dimorphism was expressed as the ratio of the mean male to female body mass for each species (see the electronic supplementary material, table S1 for references). Carnivorans (e.g. eat mostly meat), frugivores (e.g. eat mostly fruit) and gummivores (e.g. eat mostly gums and saps from trees) were in contrast to grazers, browsers, piscivores, omnivores, insectivores, herbivores and folivores (diet may also include fruits) scored as having defensible foods (see the electronic supplementary

material, table S1). We downloaded a sample of 100 phylogenetic trees from vertlife.org [76] to represent the evolutionary history of these species and its uncertainty.

(c) Statistical analyses

We modelled the probability of a species having male-biased, unbiased or female-biased leadership in both contexts using multinomial models [72,77], setting 'unbiased' as the reference level (see the electronic supplementary material for more details). For the purpose of these analyses, we treated subspecies in our database as the same species, assigning them to the same tip of the phylogeny, and, if necessary, using a species-level random effect to account for multiple observations of the same species. For further adjustments to species names to match the available phylogeny see the accompanying R code. For each context, we ran an intercept-only model (model 1), as well as a model with the predictor variables food defensibility and sexual dimorphism (model 2). Food defensibility was coded as absent (0) or present (1), and sexual dimorphism was centred on 1 (e.g. monomorphic species with males and females of the same size) and re-scaled such that units represent standard deviations. We also fitted a model including only a dummy variable for primates versus non-primates (model 3). Finally, we included sex bias in movements as a predictor of sex bias in intergroup conflicts (model 4).

We used the Bayesian regression models using the *'Stan'* package v. 2.14.4 [78] in R v. 4.0.4 [79] for all analyses, as well as some functions of the *phytools* [80], *rethinking* [81], *ape* [82] and *wesanderson* [83] packages. We looped all models over the sample of 100 trees and pooled the parameter estimates to account for phylogenetic uncertainty. In addition, we ran all models on a consensus tree, generated with the *consensus.edges()* function in *phytools*; as there were virtually no differences between these approaches, we report only the looped models representing the full phylogenetic uncertainty.

From each model, we present the mean probabilities of each type of sex bias with 95% credible intervals and calculate the degree of support for the most likely type of sex bias to have higher probability than (i) each of the other types (i.e. the probability of the difference being greater than 0) and (ii) expected by chance (i.e. the probability of a sex-bias being greater than 0.33). Rather than representing arbitrary cut-offs like conventional statistical significance, these probabilities can directly be interpreted as the quantitative support for a given hypothesis; we invite readers to judge for themselves the degree of support they find convincing. Lastly, for each model, we also calculated its phylogenetic signal, Pagel's λ (i.e. proportion of variance explained by the phylogenetic random effects [84]), though note that we had to use highly regularizing priors on the phylogenetic variance components to achieve good model convergence, which reduced λ by about half.

3. Results

Overall, we found that male-biased participation was most likely in intergroup conflict across mammals (figure 1; model 1; see also the electronic supplementary material). Specifically, participation in intergroup conflicts was more likely to be male-biased (probability of male bias = 0.60, 95% credible interval (CI) = 0.25–0.86) than female-biased (0.16, 0.02–0.37) or unbiased (0.24, 0.08–0.45), with 93%, 90% and 92% confidence that the probability of male bias was higher than that of female bias, unbiased and chance, respectively. By contrast, leadership in collective movement was more likely to be female-biased (0.51, 0.13–0.85), as opposed to male-biased (0.23, 0.03–0.46) or unbiased (0.27, 0.06–0.49), with the
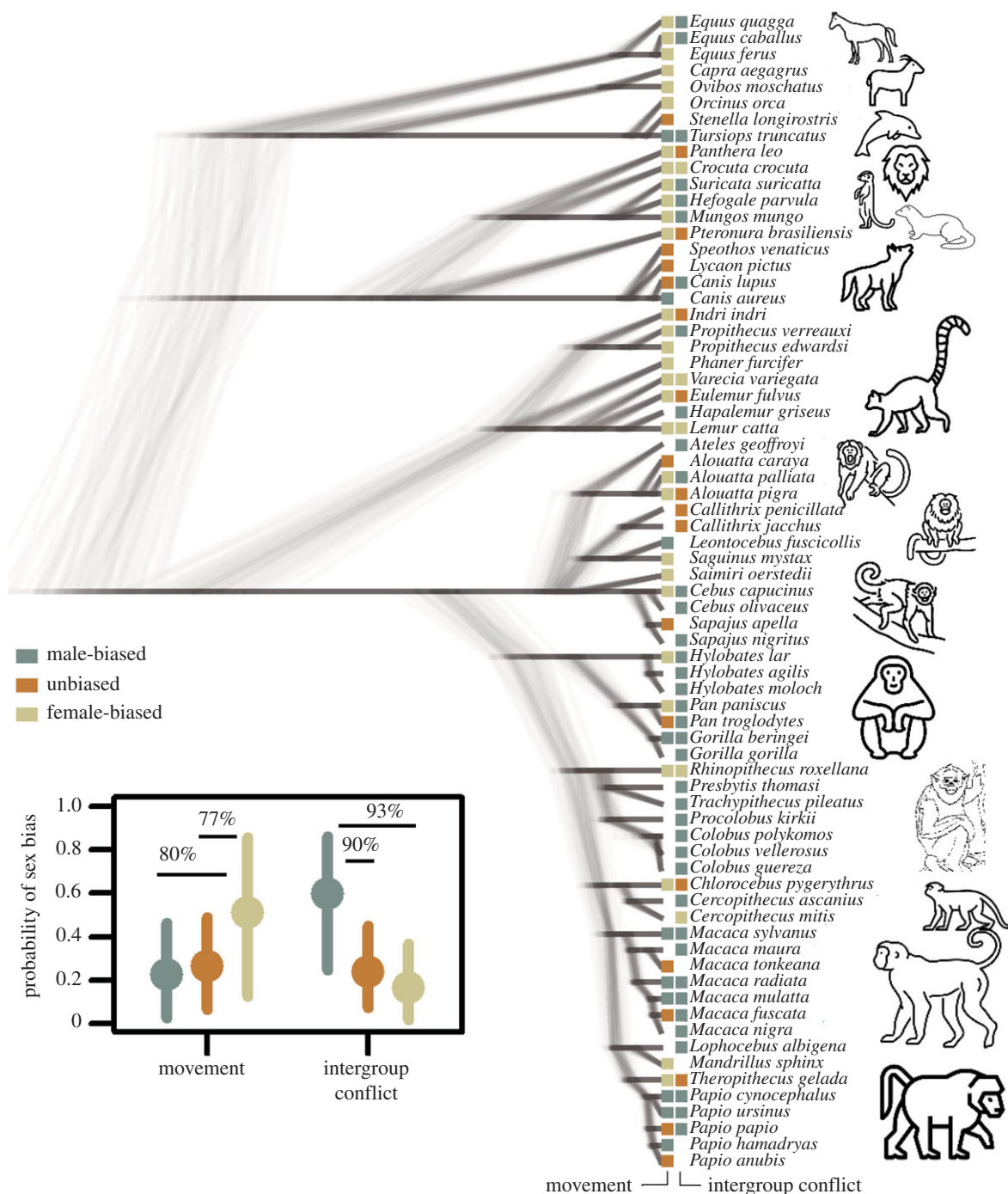
Figure 1. Phylogeny of the studied species, with observed sex bias in movement and intergroup conflict indicated by the coloured boxes at the tips. The inserted graph shows the predicted probabilities (means ± 95% credible intervals) of different types of sex bias for both contexts. The horizontal bars and percentages inside the graph indicate the degree of support for a *difference* between two probabilities, e.g. the model is 93% confident that male bias in between-group conflict participation is more likely than female bias. Species icons were downloaded from thenounproject.com. (Online version in colour.)

difference in probabilities supported with 80% and 77% confidence respectively, and female bias was higher than expected by chance with 79% confidence. There was weak phylogenetic signal in both models (mean Pagel's λ and 95% CI for intergroup conflict = 0.08, 0.00–0.27); for movement = 0.18, 0.01–0.53), somewhat reduced by strong priors on variance components, implying that this typical mammalian pattern of male-biased participation in intergroup conflict and female-biased leadership in movement also applies to some extent to ancestral species.

These results did not change fundamentally when adding sexual dimorphism and resource defensibility as predictor variables (model 2; see the electronic supplementary material for full summary). For instance, male-biased participation in

intergroup conflict was predicted to be somewhat less likely when food was defendable versus non-defendable, but with high uncertainty (mean odds ratio (OR) = 0.79, 95% CI = 0.25–1.49, probability OR less than 1 = 78%); other associations were even more uncertain. Results did also not differ qualitatively between primates and non-primates (model 3; see the electronic supplementary material). In terms of the link between sex bias across contexts (model 4), the probability of male-biased participation in intergroup conflict was reduced in species with female-biased leadership during movement (mean OR = 0.66, 95% CI = 0.18–1.29; probability OR less than 1 = 87%), though other associations were much more uncertain (e.g. greater female bias in intergroup conflict when there is female bias in movement, OR = 1.30, 95% CI = 0.33–2.60;
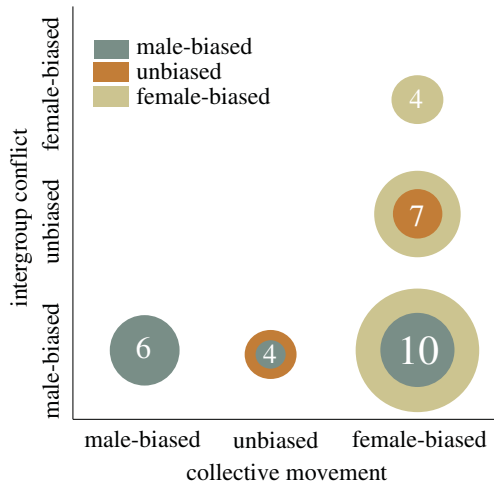
Figure 2. Distribution of sex-biased movements versus intergroup conflicts for the subset of social mammals for which data on the sexual distributions in collective action is available for both contexts. The size of each circle (and numbers inside each) reflect the numbers of species represented in each of the nine possible categories. Female-biased movements and male-biased intergroup conflict was the most common pattern ($n = 10$ species). Intergroup conflict was male-biased for all species with male-biased ($n = 6$) or unbiased ($n = 4$) leadership in movements. Female-bias in intergroup conflict ($n = 4$) or unbiased ($n = 7$) only emerged in species with a female bias in movements. (Online version in colour.)

probability OR greater than $1 = 62\%$; see the electronic supplementary material; figure 2).

4. Discussion

(a) The general pattern: male warriors in intergroup conflict

We found that male bias in intergroup conflicts was the modal pattern across social mammals, accounting for phylogeny and several covariates. This pattern seems to reflect the differential costs and benefits of participation developed in the introduction, e.g. the possibility for males to gain mating opportunities (with in-group or out-group females) or defending in-group females, outweighing whatever resource benefits females may gain, or the costs of participation being substantially higher for females. This general pattern is typified by some of the best-studied non-human primates such as chimpanzees (*Pan troglodytes*) [85,86] and mountain gorillas (*Gorilla gorilla gorilla*) [87–90] in which males are considerably larger than females and, at least in the case of gorillas, the resources that males compete over (harems of females) are much more defensible than the resources females compete over (foliage). However, it is important to note that even for these species there is some evidence for female participation in intergroup conflicts; for instance, female gorillas direct aggression towards solitary males to avoid takeovers and the subsequent risk of infanticide [87]. More generally, sexual dimorphism in our study failed to predict male bias in intergroup conflicts. In fact, adult males and females are similarly sized in many species with male bias in intergroup conflict, including meerkats (*Suricata suricatta*) [91,92], Geoffroy's spider monkeys (*Ateles geoffroyi*) [61], Zanzibar red colobus monkeys (*Piliocolobus kirkii*) [93], and Thomas's langurs (*Presbytis thomasi*) [94]. Our analyses also suggest that food defensibility plays a

minor role in shaping sex bias in intergroup conflict. In fact, species with male bias in intergroup conflicts spanned all diet types, ranging from herbivores (e.g. feral horses; *Equus caballus*) [95] to omnivores (e.g. white-faced capuchins; *Cebus capucinus*) [96,97] and carnivorans (e.g. grey wolves; *Canis lupus*) [98]. Thus, perhaps these sex differences are attributed more strongly to the differences in the costs of participation because female mammals are energetically limited by the demands of gestation, lactation and, in some species such as primates, the carrying of infants [51]. However, there was virtually no difference between primates and non-primates, hence the costs of carrying infants [51,74,99] do not seem to be a general explanation for this sex bias.

In summary, male-biased participation in intergroup conflict is the mammalian norm and most likely the ancestral pattern, which makes sense in light of differential costs and benefits. However, these costs and benefits are not well captured by our predictor variables sexual dimorphism, food defensibility or infant-carrying, hence future studies should test more nuanced predictions.

(b) The general pattern: female guides in collective movements

Our analysis demonstrated that female mammals generally serve as 'guides' in collective movements. That is, on average, females recruit followers more often than males in the context of collective group movements, accounting for phylogeny and covariates. In most mammals, females are philopatric and may have increased knowledge about local resources, resulting in more frequent initiations or leadership of group movements [58,65]. Indeed, some of the best-studied examples of collective movements include adult female zebras (*Equus burchellii*) leading groups to water holes [100] and elder (postmenopausal) female orca whales (*Orcinus orca*) leading groups to limited food resources [101]. Food defensibility, but not sexual dimorphism, further affected collective movement in that male-biased leadership was less likely when food is defendable. Our analysis also uncovered associations between sex bias across the two contexts of collective action. Specifically, male-biased participation in intergroup conflict was less likely and female-biased participation more likely (though with much greater uncertainty) in species with female leadership during collective movement.

In summary, female leadership in movements was the norm and is consistent with female philopatry and the fact that female fitness is limited by access to food. Female leadership in the movement context also seems to constrain sex-biased participation in intergroup conflict, making male bias less and female bias more likely. We discuss exceptions to the general patterns in the next section by focusing on those species with female bias during intergroup conflicts.

(c) Lessons from exceptions to the rule: the female warriors

A handful of species deviate from the modal pattern of male-biased participation in intergroup conflict which could shed additional light on the factors contributing to sex differences in this context. These 'female warriors' span four biological orders, including carnivorans and primates, suggesting independent evolutionary origins (see figure 3 for details). Whereas factors such as direct benefits, female dominance,
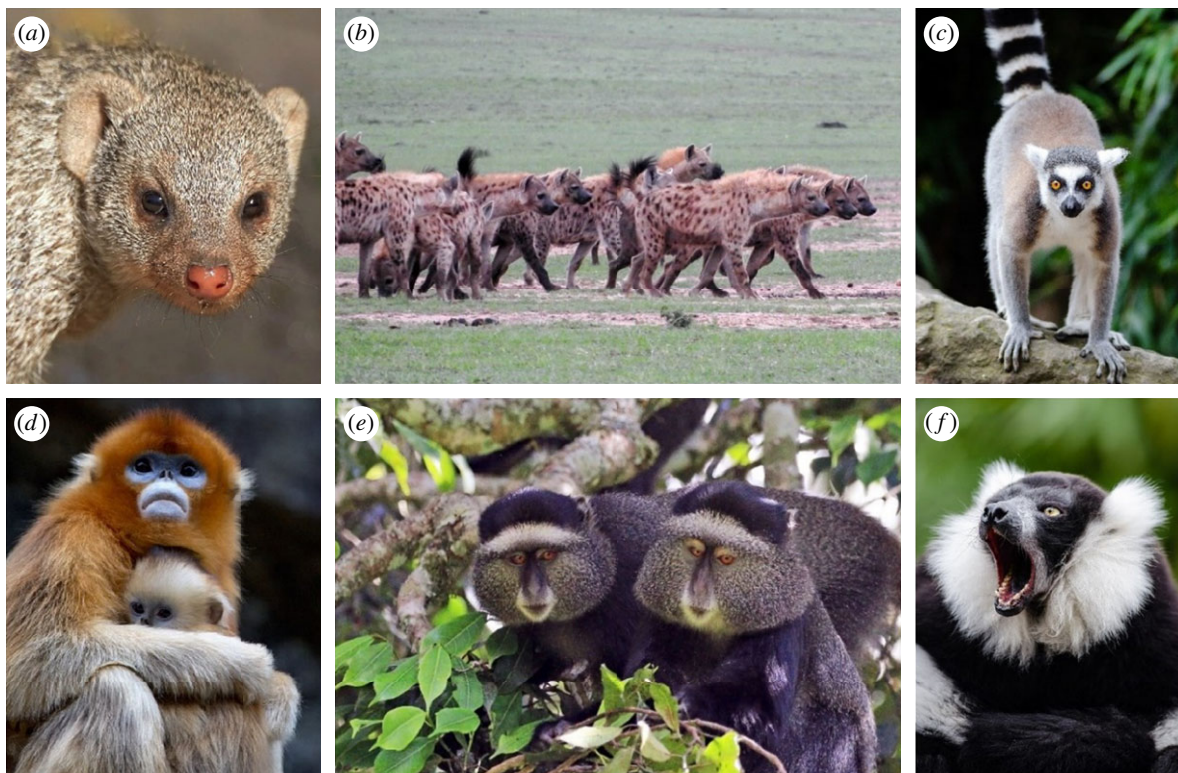
Figure 3. Female warriors among social mammals include a handful of species for which females participate in intergroup conflicts more often than do males, such as in the (*b*) spotted hyena, (*c*) ringtailed lemur, (*d*) golden snub-nosed monkey, (*e*) blue monkey and (*f*) black-and-white ruffed lemur. The (*a*) banded mongoose is also of particular note; male warriors participate in intergroup conflicts more often than females, but female banded mongooses instigate most intergroup conflicts and, therefore, disproportionally influence the initial group decision to engage in this form of collective action. Photos by Axel Tschentscher, Jack Grady and Charles J. Sharp with permission or part of the public domain. (Online version in colour.)

intense female–female competition and female-biased sex ratios within groups may facilitate or permit female-biased leadership, there appear to be many paths favouring female bias during intergroup conflicts across social mammals.

First, two plural breeding social carnivorans, banded mongooses (*Mungos mungo*) [43,102,103] and spotted hyenas (*Crocuta crocuta*) [30], experience intense female–female competition [104,105], infanticide [106,107] and territoriality [108–110], presumably owing to highly defensible food [30,111]. For both species, females instigate intergroup conflicts more than males, but only female spotted hyenas participate in conflicts at higher rates than do males. Thus, although banded mongooses fail to meet our definition of female warriors, they are still of particular note because they are exploitative leaders that instigate intergroup conflicts more than males [43]. The banded mongoose case is an important example for underscoring the critical importance of using precise definitions and consistent data collection when defining leadership (influence) versus participation (aggression) in intergroup conflicts. Interestingly, female mongooses gain direct incentives by mating with males from rival groups [43,102,103,112] and female hyenas gain more direct benefits (ephemeral, contested ungulate prey) than males from winning intergroup conflicts over territories [109,113]. High-ranking hyenas in female-dominated societies are also most often the ones charging in the front lines at intruders [30,114,115]. Black-and-white ruffed lemurs (*Varecia variegata*) [116] and ring-tailed lemurs (*Lemur catta*) [117–121] also live in female-dominated societies [122–124]; in these species females participate more and are more aggressive than males in defending fruits from intruders [116–121].

Second, female warriors also emerge in several species for which adult females are more numerically frequent than males,

which may contribute to this pattern. For example, in golden snub-nosed (*Rhinopithecus roxellana*) [125], Samango (*Cercopithecus albogularis*) [126] and blue (*Cercopithecus mitis stuhlmanni*) [127] monkeys, one adult male is associated with multiple females. However, note that one-male multi-female groups are also common in gorillas and some langurs, who do not show female-biased participation in intergroup conflict. Female sexual competition is unusually intense among snub-nosed monkeys [128]; females initiate roughly 96% of courtship attempts [129,130] and join forces to protect against infanticidal males [131]. Female–female intergroup competition for access to fruit trees is also particularly intense for blue monkeys [132–134]. Thus, intense female competition may affect sex roles in collective action.

(d) Open questions and a path forward for understanding collective action in animals

Overall, our analyses revealed that for a typical mammal, males participate more often in intergroup conflicts, and females lead more often in group movements. The patterns are generally consistent with sex-specific incentives for participation, though these are not well captured by our predictor variables of sexual dimorphism, food defensibility and infant carrying. We also found that female leadership in movements is associated with a reduced male bias and perhaps increased female bias in intergroup conflicts, suggesting some carry-over effects or constraints on leadership across these two contexts.

Our synthesis also raises many unanswered questions and there are few—if any—explanations that fit all of the species in our sample. Moreover, the available data cannot offer insights regarding whether intergroup encounters are fundamentally

motivated by attacks (expanding access to resources) or defence (protecting current resources). Distinctions between these categories could provide further insights into sex differences in the motivations to attack, presumably to expand access to resources, versus simply defending existing ones. Thus, we propose that research should inquire about this distinction to the extent possible in field observations.

Several other key questions remain. Among these are whether intergroup conflicts in animals are comparable with those of human raids or warfare in size [36,135], motivation [27], or intensity [136]. With respect to motivation and intensity, intergroup conflicts by non-human animals may be based on individual incentives rather than on the understanding of a territory as a common good [27]; yet, individuals incentives may also contribute to human warfare to some extent [137]. Moreover, factors such as the adult sex ratio or risk of infanticide, which we were unable to explicitly include in our analysis, may further contribute to sex bias in intergroup behaviours. For example, in Indo-Pacific bottlenose dolphins with intense mating competition, a skewed adult sex ratio is associated with the formation of male alliances, pronounced male bias during inter-alliance conflicts, and infanticide [138–140]. More generally, future studies should compare observed and expected frequencies of participation in intergroup conflict by both sexes based on the adult sex ratio.

We focused on participation rather than leadership in intergroup conflict owing to limited data on the latter (see §2a). Studies identifying who initiated conflicts or showing that participation of specific individuals results in the recruitment of more actively participating individuals may help us to understand whether a leadership role can also be assigned to intergroup conflicts in a practical and meaningful way. Being able to quantify collective behaviours in these ways will also be able to contribute more broadly to understanding leadership within a comparative perspective. These efforts could also help to provide more concrete information on how the fitness consequences associated with each context vary by sex and intraspecifcally among groups; robust measures of reproductive outcomes [141] that allow for comparative analysis within and across species could offer more insights.

(e) Possible implications for understanding the psychology of human collective behaviour

Our findings are consistent with the notion that male bias in participation in intergroup conflict (as seen in human warfare) has deep evolutionary roots within the mammalian lineage. Men are generally the main participants in warfare in both small-scale societies and large, industrialized societies [5,142] and the 'male warrior hypothesis' [8,143,162] was thus proposed to explain male-dominated initiation, planning and participation in intergroup aggression and its effect on psychology [40,54]. On average, men are more prejudiced against and openly hostile towards members of outgroups, for example, immigrant groups in society, and outgroup men are more likely to be the target of intergroup prejudice [8]. Men have a stronger preference than women for inequalities between groups in society (i.e. social dominance orientation [144]), and this tendency is exacerbated when they are experimentally primed with an outgroup [145]. Men cooperate more with their group than women do in economic games when their group is in competition with other groups [143], and there is some evidence that this effect is stronger for physically more formidable

men [146]. Moreover, men tend to, on average, take more risks and be more overconfident in risky situations than women [147–149], a finding consistent with evolutionary models [150]. While there is much debate about the antiquity of warfare in human history (e.g. with some arguing for a recent origin with complex foragers or the domestication of plants and animals [151,152]), our results suggest that male bias in intergroup conflict—whether considered 'warfare' or not—has deep roots in the mammalian lineage, giving it ample time to shape sex differences in intergroup psychology. Nevertheless, it is likely that certain aspects of women's psychology have also been shaped by intergroup conflict, but possibly in different ways (e.g. avoiding sexual coercion by men) and these await investigation [8].

Direct information about gender-biased leadership during collective movements in humans is limited. However, anthropological accounts of hunter-gatherer decision-making (e.g. about residential moves) generally emphasize consensus building [153,154], and models assuming gender equality in decisions regarding camp moves are most consistent with observed patterns [155]. Moreover, studies focused on leadership in human crowds in industrialized societies also usually involve mixed-gender groups and focus on how group size and uninformed individuals influence collective movements rather than gender differences in leadership [156].

Although leadership in collective movements in humans is less well studied, our findings that the sex bias among mammals is reversed between contexts are consistent with previous work on humans showing that gender-biased influence in human societies is often situational, varying across society type and organizational context [157]; for example, preferences for leaders with masculine traits are strongest during times of conflict [158,159] and conservative voters more strongly prefer masculine-looking political candidates than do more liberal voters [160]. Thus, more human studies focused on the extent of gender-biased leadership for various contexts and whether it covaries among contexts are needed. Together with our current findings, these studies could offer transdisciplinary insights [161] into the general patterns giving rise to sex differences in collective action across mammals, including humans.

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