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Sex differences in cooperative coalitions: a mammalian perspective

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In group-living species, cooperative tactics can offset asymmetries in resource-holding potential between individuals and alter the outcome of intragroup conflicts. Differences in the kinds of competitive pressures that males and females face might influence the benefits they gain from forming intragroup coalitions. We predicted that there would be a female bias in intragroup coalitions because females (1) are more like to live with kin than males are, and (2) compete over resources that are more readily shared than resources males compete over. We tested this main prediction using information about coalition formation across mammalian species and phylogenetic comparative analyses. We found that for nearly all species in which intragroup coalitions occur, members of both sexes participate, making this the typical mammalian pattern. The presence and frequency of female or male coalitions were not strongly associated with key socio-ecological factors like resource defensibility, sexual dimorphism or philopatry. This suggests that once the ability to form intragroup coalitions emerges in one sex, it is likely to emerge in the other sex as well and that there is no strong phylogenetic legacy of sex differences in this form of cooperation.

This article is part of the theme issue 'Cooperation among women: evolutionary and cross-cultural perspectives'.

> If cooperation can be analysed via natural selection operating on individuals, a new way to conceptualize the process emerges. Instead of viewing cooperation as distinct from competition, it becomes productive to regard them together. Students of animal behaviour have long recognized that an artificial dichotomy may exist insofar as animals frequently cooperate to compete with conspecifics. In taxa as diverse as insects, birds, and mammals, animals cooperate to obtain immediate or deferred fitness benefits.
>
> Muller & Mitani 2005 [1]

1. Introduction

Competition over access to resources needed for individuals to survive and reproduce successfully is ubiquitous in nature. The outcome of contests between pairs of individuals (dyads) is expected to be influenced by asymmetries in the resource-holding potential of the participants [2,3] and the associated fitness consequences of fighting [4]. Resource-holding potential is based on a combination of morphological traits such as body size and weight, the size of weaponry, including antlers, horns, tusks and canines, and physical condition, which influences endurance capacity, strength and agility. For example, male red deer (*Cervus elephas*) compete over access to groups of females during the breeding season. Body size and condition influence males' success in contests and their ability to maintain access to groups of females [5]. Both body size and antler size are positively related to males' lifetime breeding success [6]. In many group-living

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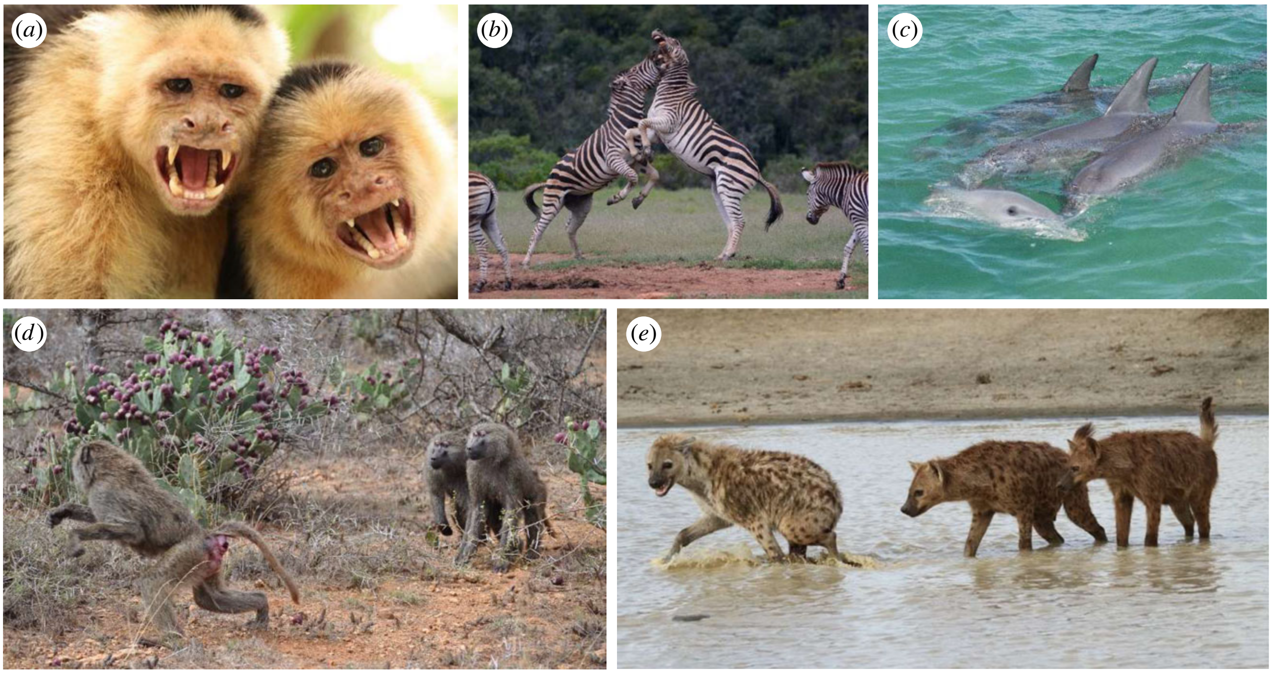

Figure 1. Numerous species of social mammals form intragroup coalitions. Intragroup coalitions involve two or more individuals joining forces to direct aggression toward another group member (*a,c–e*). Some coalitions initially also involve one individual (e.g. plains zebra in the lower right of panel *b*) joining an ongoing dyadic fight to intervene on behalf of others. For most of these species, members of both sexes form intragroup coalitions as is the case for (*a*) white-faced capuchins in Costa Rica, (*b*) plains zebra in South Africa, (*c*) olive baboons in Laikipia, Kenya and (*d*) spotted hyenas in Tanzania. Interestingly, only male (*e*) Indio-pacific bottlenose dolphins of Australia form coalitions. Male dolphins do so as part of their multifaceted set of mating strategies. Photographs reproduced with permission from Abid Karamali (Costa Rica), Kore Nordmann, Joan Silk (Uaso Ngiro Baboon Project), Oliver Höner (Ngorongoro Hyena Project) and Ewa Krzyszczyk (Shark Bay Dolphin Project).

species, stable individual differences in resource-holding potential lead to predictable outcomes of contests between pairs of individuals, and individuals can be ordered in linear dominance hierarchies [7–9]. High-ranking animals generally have priority of access to monopolizable resources, and high rank is positively correlated with reproductive success in both sexes [10].

In group-living species, cooperative tactics can offset asymmetries in resource-holding potential between individuals and can alter the outcome of intragroup conflicts. One such tactic is intragroup coalition formation (figure 1), also called agonistic aiding and coalitionary aggression, which occurs when two or more group members join forces to collectively direct aggression toward one or more members of their own social group [11,12]. For example, high-ranking male yellow baboons (*Papio cynocephalus*) and olive baboons (*Papio anubis*) mate guard sexually receptive females and prevent lower-ranking rivals from mating with them [13–15]. Sometimes two or three lower-ranking males join up to challenge a mate-guarding male that outranks them both and often succeed in defeating him [13–15]. In some species, coalitionary aggression plays an important role in the acquisition and maintenance of dominance rank. For example, in some species, females form dominance hierarchies in which maternal kin occupy adjacent ranks (e.g. spotted hyenas, *Crocuta crocuta* [16,17]; white-faced capuchins, *Cebus capucinus* [18]; and several species of cercopithecine primates [19]). Maternal rank inheritance is the product of coalitionary support from kin. Mothers and other close kin consistently support related females in conflicts against members of other matrilines, and their support enables maturing females to defeat all of the females that their maternal relatives can defeat [19]. Coalitionary outcomes can also influence male dominance rank (African wild dogs, *Lycaon pictus* [20]; chimpanzees, *Pan troglodytes* [1,21]; Assamese macaques, *Macaca assamensis* [22]; Japanese macaques, *Macaca mulatta* [23]). In bonobos, *Pan paniscus*, coalitions of adult females often outrank males, and male dominance rank [24] and male access to female mates is influenced by the presence and support of their mothers [25–27]. In many human societies, coalitions are also crucial for both men and women for gaining social status, resource access and fitness [28–33].

Differences in the kinds of competitive pressures that males and females face might influence the benefits they gain from forming coalitions with adults of the same or opposite sex in within-group conflicts. In mammalian species, the primary focus of competition for males and females often differs. For mammalian females, which bear the energetic costs of internal gestation and lactation, fitness is usually expected to be more strongly influenced by the outcome of competition over access to material resources, such as food or dens, than access to mates [10,34,36–]. The obligate commitment of mammalian females to gestation and lactation makes them a limited resource for males, and male fitness is typically more strongly affected by the outcome of competition over access to females than other kinds of resources. Because males compete for access to fertile females [34–36], sexual selection tends to favour the evolution of traits that permit males to monopolize and gain mating opportunities with females [37–40]. The resources that females compete over, such as food and safety (e.g. dens or burrows), are more readily shared than paternities [41,42], and this can make the benefits of coalitions more evenly shared for females than males [43]. In addition, kinship is the primary foundation of cooperation in mammalian groups [44], and coalitionary activity is often nepotistic [11]. It is more common for adult female mammals to live in groups with close kin than for adult males to live with kin [10]. Thus, adult females might be more likely to intervene in ongoing fights or join forces to form coalitions with other adult group members because they are more likely to live with appropriate coalition partners, particularly when competing for access to spatially clumped food [45–47]. At the same time, males may benefit from intervening in support of females if this reduces the risk that their offspring will become victims of infanticide [48] or serves as a commodity that can be exchanged for other kinds of services, such as grooming [49–51], food-sharing [52], or future mating opportunities [53–55]. In species that form multi-male groups, males' participation in coalitionary aggression against other males within the group may help them to increase or maintain high-ranking positions in the dominance hierarchy (references above) or obtain mating concessions from more powerful males [56,57]. Males may also join forces to gain direct, immediate benefits during consortships [58]. In general, male conflict is also expected to be associated with sexual size dimorphism across species [59,60], as more intense male–male competition favours larger body size and weaponry.

In mammals, males are more likely to participate in intergroup conflicts than females [61–63], but the extent to which sex differences in intragroup coalitions exist is unknown, particularly beyond primates. Sex differences in patterns of dispersal may influence the propensity for intragroup coalitions to form. Among mammals, females are typically philopatric whereas males frequently disperse at sexual maturity, although in some species neither sex, both sexes or only males are philopatric [64]. These patterns may make kin-based coalitions more common among females than males [35,44,45,65,66]. However, coalitions are not limited to genetic relatives [11]; chimpanzee and bonobo females form intragroup coalitions even though females are the dispersing sex [67,68] (see also [69]). In some species, males do not limit coalitionary support to kin (e.g. chimpanzees [70], dolphins [71], stump-tailed macaques (*Macaca artoides*) [72]).

The goal of this paper is to evaluate sex differences in coalition formation during intragroup conflicts across social mammals. Whereas intergroup coalitions are well-recognized across taxa from ants and fiddler crabs to humans [61,73,74], historically, research on intragroup coalitions has focused primarily on primates, giving rise to the notion that intragroup coalitions may be more complex and frequent among primates than non-primates [75]. However, if the factors governing coalition formation are generalizable to social mammals overall, then we expected these patterns to be robust for primates and non-primate mammalian species. We hypothesized that females would cooperate in intragroup coalitions in more species than males because (1) females are more likely to live with kin than males are, and (2) the resources that females compete over are more readily shared than the resources that males compete over. We predicted that this would produce robust sex differences in intragroup coalitions even after controlling for shared phylogenetic history across the mammalian lineage. We also predicted that coalition formation would be more common in the philopatric sex than in the dispersing sex, and that female coalition formation should be present most often in species that rely on foods that can be monopolized and defended than in species that rely on foods that cannot be monopolized and defended. Finally, we predicted that males should form coalitions most often in species for which competition over access to females is most intense. Because the intensity of male–male competition is associated with sexual dimorphism in mammals, we predicted that the presence of male intragroup coalitions would be positively associated with the extent of sexual dimorphism in body size.

2. Methods

(a) Literature search and data collection

To capture the breadth of empirical studies focusing on coalitions in non-human mammals, this study builds upon an initial review of intragroup coalition formation in group-living mammals [11], papers citing this review, including [43,76], and other papers identified via Google Scholar searches for species that engage in intragroup coalitions. We also communicated directly with researchers working on species for which there are reports of intragroup coalitions in one sex, but no information about the other sex. Captive studies were retained in our analysis to expand the number of species that we were able to include in the analyses. Although captivity is likely to influence the context and frequency of coalitions, it seems unlikely to generate false positives, i.e. produce evidence of coalitions in sexes/species where they are actually absent. Domesticated species were excluded from the analysis.

We scored each species as showing evidence of coalitions by females, males or both based upon whether or not adults of the focal sex intervened in ongoing fights on behalf of, and/or simultaneously formed coalitions to support, adult recipients of any sex. Specifically, same-sex and mixed-sex coalitions were both included as evidence for coalition formation for the focal sex. For example, male donors were scored as engaging in coalitions if males intervened on behalf of female recipients, male recipients, or both. This was used to assess the general pattern of sex differences in coalition formation, and also re-coded into presence/absence of female and male coalitions, respectively, as described below. In addition to presence/absence, a measure of the *frequency* of coalition formation by each sex was desirable. However, comparative data on the relative frequency of intragroup coalitions formed by each sex are rare, and this makes the direct assessment of coalition frequency by sex challenging. Ideally, each study would report on focal data collected on both sexes, making it possible to estimate the rate of coalition formation (events/time observed). Even then, it is not clear whether the relevant comparison would be based on *per capita* rates by males and females, or the absolute rates summed across individuals of each sex, or whether rates of coalition formation ought to be corrected for opportunities to intervene, which is a function of the frequency of aggression. Because coalitions are generally uncommon, almost all studies rely on ad libitum data or some combination of focal and ad libitum data, and these kinds of data are biased by differences in observability, conspicuousness and observer focus.

We attempted to overcome these methodological issues by implementing a bibliometric approach to assess the relative frequency of intragroup coalitions by sex. For each sex, we assessed whether intragroup coalitions are absent, present, or common for any species for which there is evidence that members of at least one sex are known to form intragroup coalitions. For example, females of a species were scored in one of the three following ways: (i) female coalitions are absent if there are papers mentioning male intragroup coalitions (i.e. somebody had studied coalitions in this species) but none mention female intragroup coalitions (or explicitly say that they are absent), (ii) female intragroup coalitions present if there is at least one study describing female intragroup coalitions, or (iii) female coalitions common if there are two or more published empirical studies describing female intragroup coalitions; the bibliometric method credits the number of original studies as evidence for the importance/frequency of a phenomenon.

We limited publication counts to original empirical studies, including dissertations and master's theses; review papers were omitted from these counts. Species for which intragroup coalitions by males or females were simply documented as an observation (but with no data analysis) in a published study or via personal communication with researchers were also deemed to be present (but uncommon) for a species if no additional published accounts were available. Information from multiple studies was typically combined to make this assignment. In most cases, a single study focused only on intrasexual coalition formation.

We used the two-step ratio [77] to assign sexual dimorphism using mean male and female body masses for each species (see electronic supplementary material, table S1 for references) [77]. Carnivores (i.e.. eat mostly meat), frugivores (i.e. eat mostly fruit) and gummivores (i.e. eat mostly gums and saps from trees) were scored as eating defensible food. Grazers, browsers, piscivores, omnivores, insectivores, herbivores and folivores (diet may also include fruits) were scored as eating non-defensible foods (see electronic supplementary material, table S1). We also described species based on patterns of philopatry (females only, males only, both sexes, or neither sex), adult integration of the sexes (mixed groups or sexually segregated) and presence of adults by sex (multiple males and/or females within groups; see electronic supplementary material, table S1 for references). A sample of 100 phylogenetic trees from VertLife.org [78] was downloaded to represent the evolutionary history of these species and its uncertainty.

(b) Statistical analyses

To assess the general patterns of coalition formation by sex, i.e. to model the probability of female coalitions, male coalitions and coalitions by both sexes in a typical mammal, we used multinomial models, first only with an intercept (Model 1) and then with predictors to distinguish sex-segregated species from those living in mixed-sex groups (Model 2), and primates from non-primates (Model 3). To test socio-ecological predictors we used binomial models for the presence and absence of female coalitions (Model 4) and male coalitions (Model 5), and coded food defensibility as present (1) or absent (0) and centred sexual dimorphism on 1 (e.g. male and females of the same size). Philopatry was coded as 'females philopatric', 'males philopatric', 'both sexes philopatric' or 'neither sex philopatric'. Finally, we repeated models 4 and 5 using our ordinal measure of coalition frequency with cumulative logit distributions.

These models were implemented as Bayesian phylogenetic generalized linear mixed models (GLMMs) [79] in R 4.2.0. [80] using the *brms* package v. 2.14.4 [81]. We also used functions from the *phytools* [82], *rethinking* [83], *ape* [84] and *metbrewer* [85] packages. To account for phylogenetic uncertainty, we looped all models over the sample of 100 phylogenetic trees and pooled the parameter estimates. Bayesian models yield a posterior probability distribution for each estimated parameter, which we here summarize by its median and 90% credible intervals; to directly quantify support for specific predictions, we report the proportion of the posterior that is consistent with the prediction. For instance, to test whether female coalitions are more likely in primates compared with non-primates, the model yields a posterior distribution of the difference between the probability of female coalitions in primates versus non-primates, which we expressed as an odds ratio (OR); the proportion of the posterior that lies above an OR of 1 quantifies the degree of support for the prediction. We calculated the phylogenetic signal as an intra-class correlation, i.e. the proportion of the total variance captured by the phylogenetic random effect [79,86], which is equivalent to Pagel's λ.

3. Results

This study yielded evidence for intragroup coalitions in a total of 58 species, roughly two-thirds of which were primates (figure 2; electronic supplementary material, table S1). These species spanned five biological orders within the class Mammalia, including seven Artiodactyla (three species of deer and sheep, three dolphin species, and a peccary), three Perissodactyla (two species of horses and one zebra species), Proboscidea (one species of elephant), eight Carnivora (two species of dogs, one cat species, two species of mongooses, one hyena species and two species of coatis) and 39 Primata (39 species of primates). Roughly two-thirds of primate species reported to engage in intragroup coalitions belonged to the family Cercopithecidae (23 species of macaques and baboons). We also located primate data on intragroup coalitions formed by two species of lemurs, three species of spider and howler monkeys, seven species of capuchin and squirrel monkeys, and four species of apes.

We used multinomial models to estimate the overall predicted probabilities of coalitions by females only, males only or both sexes. Contrary to our first prediction, female-only coalitions were not more likely than male-only coalitions (figure 1, Model 1). In fact, the probability of female-only coalitions in a typical mammal (median = 0.18, 90% credible interval = 0.01–0.47) was lower than the probability of male-only coalitions (0.33, 0.04–0.67) and the most likely state was coalitions by both sexes (0.41, 0.14–0.68). Thus, only 34% of the posterior probability supported our prediction of female-only coalitions being more likely than male-only coalitions. The phylogenetic signal was moderate (median $\lambda = 0.34$, 90% CI = 0.14–0.54). In sum, conditional on having any coalitions at all, the typical extant mammal is just as likely to have female-only, male-only or both-sex coalitions.

This general pattern did not change appreciably when comparing species living in mixed-sex groups ($n = 54$ species) with sex-segregated ones ($n = 4$ species; Model 2), or primates ($n = 39$ species) with non-primates ($n = 19$ species; Model 3). Specifically, the odds of female-only coalitions and male-only coalitions were nearly the same in sex-segregated species compared with mixed-sex species (females only: median OR = 1.11, 90% CI = 0.35–2.15, probability OR > 1 = 58%; males only: median OR = 1.03, 90% CI = 0.32–2.02, probability OR > 1 = 53%) or primates compared with non-primates (females only: median OR = 0.93, 90% CI = 0.3–1.8, probability OR > 1 = 44%; males only: median OR = 1.01, 90% CI = 0.31–1.97, probability OR > 1 = 51%). We, therefore, did not stratify our subsequent analyses by these variables.

To test socio-ecological predictions about female coalitions, we combined the three categories 'females only', 'males only' and 'both sexes' into a binary variable for the presence (females only' or 'both sexes) or absence (males only) of female coalitions; philopatry was also re-coded as a binary variable indicating presence (females or both sexes philopatric) or absence (males or neither sex philopatric) of female philopatry. To test predictions about male coalitions, we analogously re-coded male coalitions as present (males only or both sexes) or absent (females only) and male philopatry as present (males or both sexes philopatric) or absent (females or neither sex philopatric). We then ran binomial models on the presence of female coalitions (Model 4), including food defensibility (yes/no) and female philopatry (yes/no) as predictors, and on the presence of male coalitions (Model 5), including

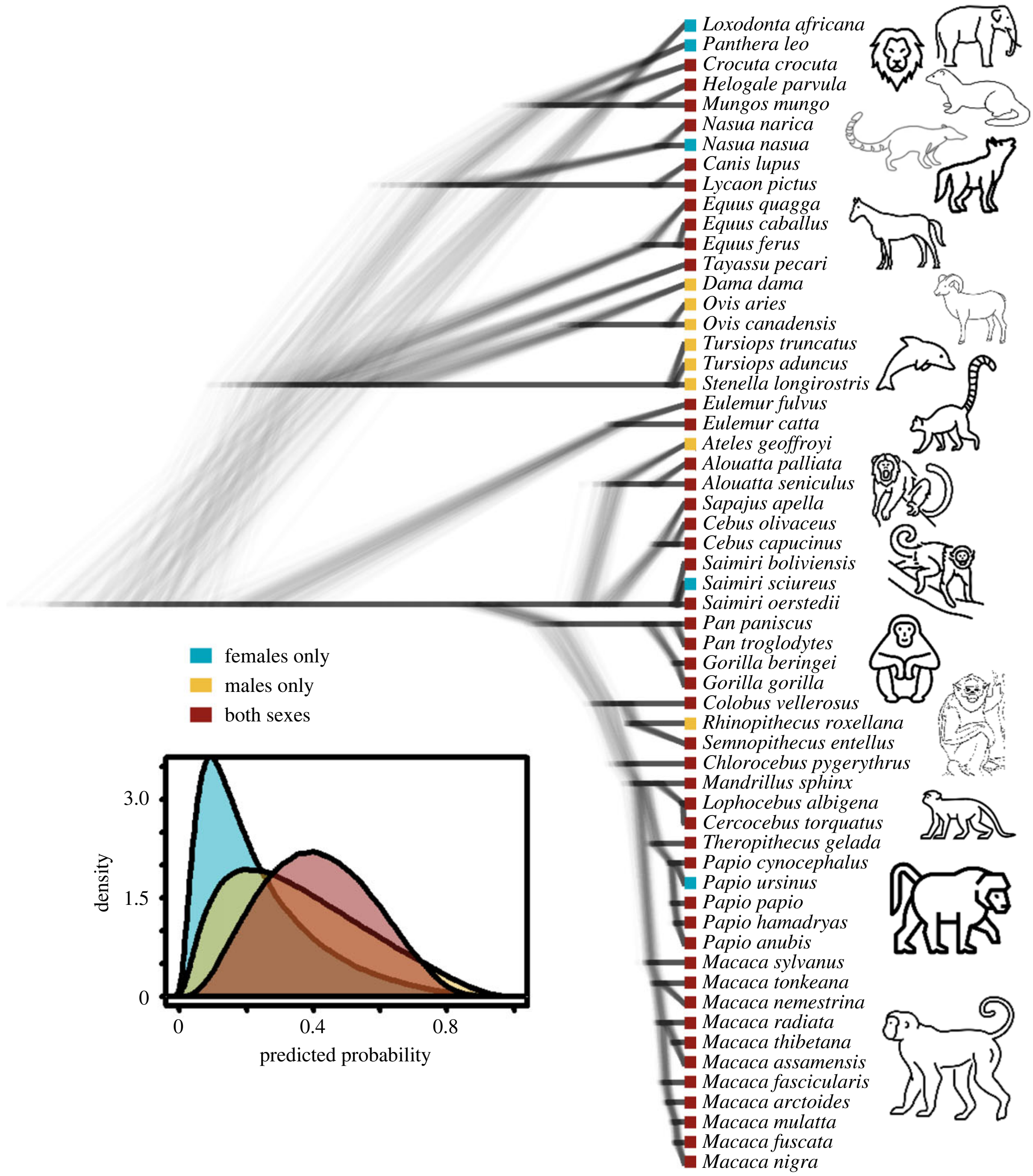

Figure 2. Phylogeny of 58 non-human social mammals that engage in intragroup coalition formation, showing some uncertainty in tree topology. The squares at the tips of the phylogeny indicate observed patterns of coalition formation: blue = females only, yellow = males only, red = both sexes. The inserted figure shows the posterior probability distributions for each type of coalition from Model 1, indicating the phylogenetic average, or typical mammalian species. Source for species icons: thenounproject.com.

sexual dimorphism and male philopatry (yes/no) as predictors. As a robustness check, we also modelled each of these competing causes on its own.

The probability of female coalitions was not higher in species with defensible food resources compared with species with non-defensible food resources (OR = 0.95, 90% CI = 0.3–1.85, probability OR > 1 = 46%), or in species with female philopatry compared with female dispersal (OR = 1.13, 90% CI = 0.36–2.18, probability OR > 1 = 59%). Likewise, the probability of male coalitions was not higher in sexually dimorphic species (OR for 1 unit change in dimorphism = 0.83, 90% CI = 0.28–1.61, probability OR > 1 = 36%), and was virtually the same whether males were philopatric or males dispersed (OR = 1.17, 90% CI = 0.39–2.21, probability OR > 1 = 63%). These inferences did not change when considering each predictor in a model on its own (see electronic supplementary material). Thus, the probability of female or male coalitions was not strongly associated with our predictors.

Finally, we tested socio-ecological predictors on coalition frequency—rather than just presence/absence—by analysing our ordinal scale data (absent, present, common) using cumulative logit distributions and the same predictors as Models 4 and 5. The frequency of female coalitions was not higher in species with defensible food resources compared with species with non-defensible food resources (OR = 0.76, 90% CI = 0.28–1.37, probability OR > 1 = 26%), though it was somewhat higher in species with female philopatry compared with female dispersal (OR = 1.47, 90% CI = 0.53–2.68, probability OR > 1 = 81%). Likewise, the frequency of male coalitions was not higher in sexually dimorphic species (OR for 1 unit change in dimorphism = 0.94, 90% CI = 0.34–1.7, probability OR > 1 = 44%), but somewhat higher in species with male philopatry compared with male dispersal (OR = 1.29, 90% CI = 0.51–2.27, probability OR > 1 = 73%).

4. Discussion

(a) General patterns regarding sex bias in coalition formation

The comparative phylogenetic analysis indicates that among species that form intragroup coalitions, the typical pattern is for members of both sexes to form coalitions. These findings are quite consistent across taxa and were not influenced by food distribution, or the extent of sexual dimorphism. There was some rather weak support for dispersal patterns to be associated with the frequency of coalitions (with 81% confidence for female, and 73% for male coalitions), but not the presence/absence of coalitions. Thus, socio-ecology did not strongly affect coalition formation.

Sex bias in coalition formation was mainly clustered within the lineage that includes ungulates and dolphins. Although intragroup coalitions have been documented in relatively few ungulates and dolphin species, even-toed ungulates and dolphins accounted for 75% of the species in which only males form coalitions. Only males formed intragroup coalitions for fallow deer (*Dama dama*) [87–91], feral sheep (*Ovis aries*) [92], bighorn sheep (*Ovis canadensis*) [93], common bottlenose dolphins (*Tursiops truncatus*) [94], Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) [[58,95,97] and Hawaiian spinner dolphins (*Stenella l. longirostris*) [98]. In all of these taxa, males formed coalitions primarily to protect groups of females from other males and to increase access to mating opportunities with females. Male Indo-Pacific bottlenose dolphins in Shark Bay, Australia are well known for forming complex, multilevel alliances to herd (female) mating partners [58]. Interestingly, although female Indo-Pacific dolphins do not engage in coalitionary aggression, non-cycling females do place their pelvic fins on the side of cycling females to initiate polyadic affiliative interactions with cycling females being harassed by males [99]. The odd-toed ungulates may represent an exception to this pattern of male-only coalition formation. Specifically, the dataset includes three odd-toed ungulate species in the family Equidae: the Przewalski horse (*ferus przewalskii*) [100,101], the wild horse (*Equus caballus*) [102–104] and the plains zebra (*Equus burchellii quagga*) [105,106]. In all three of these species, both sexes form coalitions. Males primarily intervene to interfere with other males' courtship while females most often intervene on behalf of their calves or other mares.

Outside of the ungulates and dolphins, there are relatively few species in which only one sex forms coalitions. An early account suggests that female African lions (*Panthera leo leo*) join forces to protect their offspring [107], but coalition formation has not been the subject of systematic study in lions [108]. Pairs of male lions that team up to compete against outside males for access to females are sometimes referred to as stable 'coalitions' (also called 'alliances'), but to our knowledge male lions do not participate in intragroup coalitionary aggression [109,110]. Among another social carnivoran, ring-tailed coati (*Nasua nasua*) [111–113] adult females but not males form intragroup coalitions, generally to intervene on behalf of their juvenile offspring. Finally, female African bush elephants (*Loxodonta africana*) form intragroup coalitions to protect their offspring [114,115], but male elephants do not participate in intragroup coalitions. This may be related to the fact that bachelor males spend much of their time alone and, thus, have relatively few opportunities to form intragroup coalitions.

Among the 39 species of primates included in our dataset; intragroup coalitions were found within both sexes for most species (90%). Male-only and female-only coalitions are reported to occur in a maximum of two species for each sex. Only males form coalitions in spider monkeys (*Ateles geoffroyi*) [116–118] and golden snub-nosed monkeys (*Rhinopithecus roxellana*) [119]. In spider monkeys, the absence of female coalitions may be related to the fact that mixed-sex groups often split into temporary sexually segregated subgroups, and adult females typically travel alone or with their offspring [118]. Golden snub-nosed monkeys live in one-male, multi-female groups and female–female competition is intense [119]. One captive study reported that males frequently intervened in conflicts among females, but females did not form coalitions [119]. In snub-nosed monkeys, although females do not form coalitions with each other or simultaneously join forces with males to target other females, males frequently intervene in agonistic disputes to reduce conflict among females. In one study, males intervened in 93.6% of female fights [119]. Support from males reduces female infanticide prior to mothers transferring with their infants to an outside social unit [120]. Interestingly, female snub-nosed monkeys deviate from the typical mammalian pattern of male-biased participation in intergroup conflicts [61] as females join forces to attack outside males that pose an infanticidal risk to their infants [121]. By contrast, only females form intragroup coalitions in the chacma baboon (*Papio ursinus*), although their occurrence is apparently uncommon [122,123]. Nonetheless, these low rates of coalitionary interventions are likely sufficient to reinforce existing dominance rank relationships, as is the case for yellow baboons (*Papio cynocephalus*) [124]. Strikingly, multiple studies have explicitly documented the absence of male coalitions forming to take over consortships in chacma baboons [125,126]. Finally, in Guianan squirrel monkeys (*Saimiri sciureus*), only females form intragroup coalitions to support their kin in fights over food [127]; roughly 50% of aggressive interactions in fruiting trees involved coalition formation.

(b) Limited evidence for intragroup coalitions at contested resources

We predicted that females would form coalitions more often than males because the resources that females compete over (e.g. food, dens) are more readily shared than the resources that males compete over (paternities). This prediction is supported by game-theoretical models that predict coalitions will evolve within groups when coalitionary strategies maximize individual fitness through competition for limited material resources [128]. Specifically, individuals are expected to join forces in coalitions when two or more group members may together increase each individual's chance of accessing a resource [129]. Coalitions are expected for species in which the strength of contestants is a highly reliable predictor of fight outcomes [130] and access to the rewards gained from winning [131]. Indeed, intergroup conflicts often occur directly over contested resources, including territories and resources contained within them (e.g. food, mates [61]).

Despite these theoretical predictions, empirical evidence for intragroup coalitionary aggression occurring directly over mates or food—for adults of either sex—is surprisingly limited. Instead, most intragroup coalitions form outside of circumstances involving an immediately contested resource [132]. On the whole, examples of coalitionary aggression that directly affect access to mates or food are limited. However, in male olive and yellow baboons and Barbary macaques [15,133,134], low- and mid-ranking males may join forces against higher-ranking males to take over a consortship, and male chimpanzees sometimes form coalitions to guard mates [135]. Male Camargue horses [103], Indo-Pacific bottlenose dolphins [97], and stump-tailed macaques [72] also form intragroup coalitions, often with non-kin, to gain access to sexually receptive females. However, in some cases, such as male fallow deer, coalition frequency fails to predict mating success [89]. Similarly, evidence for coalitions forming within the context of feeding competition is relatively sparse. Intragroup coalitions do increase the immediate access to food for female squirrel monkeys (*Saimiri sciureus*) [127], capuchin monkeys [136,137], savannah baboons [15], Barbary macaques [134] and chimpanzees [135]. Vervet monkeys of both sexes also form intragroup coalitions over food [137]. By contrast, spotted hyenas are significantly *less* likely to form coalitions when food is immediately available and coalitions that occur when food is available do not increase immediate feeding opportunities for coalitionary allies [11]. In many species, as in bonobos [25] and baboons [138], female coalitions, however, do protect females from male harassment or infanticide. Although intragroup coalitions often form in the absence of immediately contested resources, as we discuss in the next section, this form of cooperation can still have profound effects on the social structure (i.e. dominance status, social bonds) that in turn influence resource access in future situations.

(c) Coalitions reinforce agonistic and affiliative social relationships

Detailed descriptions of coalition formation in the literature indicate that primates and non-primates gain direct as well as indirect benefits from forming coalitions. Mammalian coalitions are used widely to reinforce the *status quo* for species with dominance hierarchies [11], with examples ranging from carnivorans (e.g. spotted hyenas [16,139,140], African wild dogs (*L. pictus*) [20]) to ungulates (e.g. fallow deer [88]) and many species of primates (e.g. Assamese macaques [22], chimpanzees [21,141]). Across species, mammals also generally bias coalitionary support in favour of kin versus non-kin [11,44,142,143]. For instance, adult female baboons [124], and spotted hyenas [11] selectively support closely related maternal and paternal kin against less closely related kin and non-kin. Similarly, male white-lipped peccaries (*Tayassu pecari*) intervene more often on behalf of their closest genetic relatives during ongoing fights [144]. Male Barbary macaques are also more likely to respond to solicitations for support from (unrelated) males with whom they have close social bonds than from males with whom they have weak ties [145]. The finding that intragroup coalitions rarely form directly over access to contested resources (e.g. food, mates)—but rather generally serve to reinforce agonistic and affiliative social relationships within both sexes—runs counter to the assumptions of most theoretical models (see previous section) and likely contributes to the general lack of intraspecific sex differences in the tendency to form coalitions revealed in this study. That is, if the primary function of coalitions is to reinforce dominance status, and both sexes benefit from high rank, then this may explain why we found little evidence of sex biases in coalition formation.

(d) Cognitive constraints and socio-ecological effects on coalition formation

The finding that members of both sexes usually form coalitions in species in which coalitions are observed suggests that the presence or absence of coalitionary behaviour may be more closely linked to species-level traits such as cognitive abilities, social organization and ecological factors than to sex differences in the benefits derived from coalitions. With regards to cognition, the constraints on intragroup coalitions may indeed differ from those of intergroup coalitions. Intergroup coalition formation likely requires an understanding of 'us versus them' and relative numbers and/or collective resource-holding power of the opposing group whereas intragroup coalitions may include 'political' decisions such as triadic awareness of rank, kinship or relationship quality.

Coalitions involve at least three parties, and individuals' decisions about whether to become involved in a coalition or who to support in an ongoing interaction may rely on simple heuristics (e.g. always support kin) or more complex calculus that integrates multiple costs and benefits (e.g. integrated knowledge of kinship, dominance rank and previous social history) [146–148]. Selective pressures requiring individuals to integrate third-party relationships based on two or more criteria (e.g. social rank and kinship) may favour the evolution of increased cognitive skills [149]. The social relationships among mammals are particularly multifaceted in groups of animals with dominance hierarchies and low average relatedness among adult females, as reflected by increases in conflicts of interest among group members, rates of coalition formation and brain sizes [76,150]. There is evidence that coalitionary behaviour is influenced by leverage and knowledge of the nature of relationships among other members of the group [125,131,132]. For example, male bonnet macaques (*Macaca radiata*) and stump-tailed macaques selectively recruit allies that outrank themselves and their opponents [125,131]. Similarly, spotted hyenas consistently intervene in fights to support the higher-ranking of two contestants, even when the dominant individual is losing [151]. All three of these species also preferentially support kin in intragroup coalitions [11]. Finally, revolutionary or levelling coalitions occur when both partners rank below their target, and can involve enormous immediate risks—but potentially high payoffs—and these forms of manipulation likely require sophisticated understanding of social dynamics [43,152,153].

The notion that cognitive constraints limit coalition formation is highly contested [12]. First, among male primates, measures of brain size fail to predict the *intensity* of coalition formation. Instead, the frequency of male coalitions in primates is best explained by their social organization (e.g. large group sizes, reduced contest competition) [154]. Second, in many species, patterns of coalition formation are explained by a simple set of rules and do not require complex social cognition. For example, simple rules of thumb could underlie the nepotistic patterns of support that are observed in many taxa. In many species, winner and loser effects occur, such that the winner of a fight is more likely to win again whereas the individual that lost a fight is more likely to lose in subsequent fights [8]. This phenomenon explains third-party interventions by fallow deer [87]; rates of coalition formation are predicted by the number of unique opponents encountered per day rather than more nuanced social measures requiring mental bookkeeping [89]. Moreover, male olive baboons form alliances with males close in rank to themselves to take over consortships from higher-ranking males [13], and partner choice may rely on males' knowledge of their own rank relationships with other males [15], not third-party knowledge of rank relationships.

(e) Limitations of the study

It is important to acknowledge that information about intragroup coalition formation is not available for many mammalian species that form social groups and could potentially form intragroup coalitions. Although coalitions are relatively conspicuous events, they are uncommon and difficult to study systematically. This means that they may occur in some species even though they have not been described in the literature.

Another limitation of our study is that the data are limited to those species for which individuals of at least one sex formed coalitions. Future analyses are needed to uncover if and how these mammalian species systematically differ from those for which intragroup coalitions are truly absent. It is possible that there are sex differences in the pattern, frequency and consequences of intragroup coalitions not uncovered in the current study. For example, male gorillas [155], bonobos [67,156] and spotted hyenas [11] form coalitions less often than females do. Moreover, additional sex differences may be detected from comparisons limited to patterns of intrasexual coalition formation. Our bibliometric measure of coalition frequency likely falls short of capturing some sex differences. Further empirical work is needed to address these issues.

(f) Conclusions

Current evidence suggests that both sexes participate in coalitions in most mammalian species in which coalitions occur, and this is not clearly influenced by dispersal patterns, the extent of sexual dimorphism, or the distribution of food resources. Taken together, this suggests that there is not a strong phylogenetic legacy of sex differences in this form of cooperation. This contrasts with participation in intergroup conflict, which is strongly male-biased in mammals, including humans [61].

Animal ethics

No new data were collected from animals for this current study.

Data accessibility. All data and R code to reproduce the results are publicly available at https://github.com/adrianjaeggi/Coalitions-by-sex-mammals.

The data are also provided in the electronic supplementary material [157].

Authors' contributions. J.E.S.: conceptualization, data curation, methodology, project administration, supervision, validation, writing—original draft, writing—review and editing; A.V.J.: formal analysis, visualization, writing—original draft, writing—review and editing; R.K.H.: data curation, writing—review and editing; J.B.S.: data curation, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed herein.

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