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Male anti-predation services in primates as costly signalling? A comparative analysis and review

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Abstract

In species in which adults of the two sexes show long-term association, males often engage in acts of assistance (“services”) aimed at females and/or their young in various behavioural contexts that are not reciprocated. We conducted a quantitative review of the primate literature on sex differences in involvement in protection against predation. We found that males were more likely to be at the front of group progressions, especially in contexts of increased risk, were more vigilant, sometimes to the point of becoming sentinels, were more active in mobbing, and were far more likely to counter-attack felids and monkey-eating raptors than females did. Our evaluation showed that these services may be an expression of male parental care or aimed at bonded partners, but we also encountered many cases in which non-sires, unrelated to either females or immatures, provide them. We hence investigate explanations invoking group augmentation or costly signalling. Currently, available data on male anti-predation services in nonhuman primates do not allow us to distinguish among them, although costly signalling better explains data on birds and humans. We develop predictions that will allow more detailed tests of the various hypotheses for this understudied phenomenon.

KEYWORDS

competitive altruism, group augmentation, mobbing, reciprocity, sexual selection, vigilance

1 | INTRODUCTION

Early field studies of the behaviour of nonhuman primates drew attention to the prominent role of adult males in predation avoidance. DeVore and Washburn (1963; see also Maxim & Buettner-Janusch, 1963) stressed how baboon troops formed a clear travel formation with adult males at the front, flanks and the rear. Males were also reported to interpose themselves in prominent locations between the group and an approaching threat (Hall, 1960). When predators attacked, multiple males were observed engaging in joint counter-attacks (review: Cowlshaw, 1994). The earlier authors interpreted this pattern as an adaptation that maximizes

the survival of the group, with expendable males protecting the valuable core of the reproducing females and their offspring. With the rejection of classic group selection (Williams, 1966), this interpretation was no longer tenable, but curiously also meant that interest in the phenomenon waned. Even so, more recent studies also suggest that males appear to be systematically more actively involved in predation avoidance than females, from vigilance and alarm calling to mobbing and counter-attack (Arlet & Isbell, 2009; Cowlshaw, 1994; Dolotovskaya et al., 2019; Iwamoto et al., 1996; Quattara et al., 2009; Stephan & Zuberbühler, 2016; van Schaik & van Noordwijk, 1989). Given that these behaviours are costly and can be risky, resulting in decreased foraging time, injury or even

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death (Caro, 2005), they require an explanation, provided they can be confirmed as being systematic.

A parsimonious modern explanation would be that these male services are made possible by the year-round association of males and females and that the males providing them are close relatives of the individuals they protect, usually the sires. If the recipients are relatives of the service providers and if Hamilton's inequality is met on average (Hamilton, 1964), the latter benefit through an increase in inclusive fitness. Since adult males in most primate species are not closely related to the females with whom they associate (Pusey & Wolf, 1996), this implies that males primarily protect their offspring. Thus, parental care has become the implicit default explanation. In most reported cases of anti-predator protection, however, the likely number of offspring sired by the males engaged in these behaviours was not known or not reported. In fact, one aim of this review is to assess whether the primate literature contains enough cases where we can exclude parental care as the explanation. While this would not exclude it as a partial explanation, it would suggest that additional explanations need to be pursued. By developing these, we will also identify the variables that must be assessed in the published cases or by future studies.

Another plausible modern interpretation is that these services are part of reciprocal relationships, in which males provide anti-predation services and females reciprocate in other behavioural currencies such as grooming. Such exchanges could in principle follow the logic of reciprocity in an iterated prisoner's dilemma (Axelrod & Hamilton, 1981). However, as group-living animals may actually have some choice between potential partners in a biological market (Noë & Hammerstein, 1995), an important consequence seems to be the establishment of more exclusive relationships, that is social bonds. Social bonds provide the context for stable relationships with relaxed reciprocity and some level of asymmetry, as confirmed by both correlational (Schino et al., 2007, 2009) and experimental (Borgeaud & Bshary, 2015; Cheney et al., 2010; Schweinfurth & Taborsky, 2018) studies. Thus, helping in social bonds becomes to some degree mutually advantageous as partners have built up a stake in each other's wellbeing (Eshel & Shaked, 2001; Roberts, 2005). This interpretation predicts that males preferably, and perhaps exclusively, aid bonded

female partners and their offspring. However, the anti-predator services often provide public benefits and thus benefit many beyond closely bonded individuals.

If at least some well-documented cases reveal that male parental care, direct reciprocity and/or interdependency do fully explain all instances of male services, we must also entertain additional hypotheses. Here, we consider two additional models: group augmentation and reputation-based partner choice, or costly signalling (see Figure 1).

Male services may benefit the actors via a process called "group augmentation" (Kokko et al., 2001). The idea is simply that the male services may yield a variety of inherent benefits to the actors. For example, the recipients' increased survival will provide anti-predation benefits due to a greater dilution of risk, greater confusion effects during flight, or improved vigilance and early detection of predators. Furthermore, the recipients of services may be able to contribute more to territory defence against neighbouring groups or interspecific competitors. Such benefits of male services are public goods that benefit all group members, which would imply that the provisioning of services is under negative frequency-dependent selection, a dynamic that is captured by the so-called volunteer's dilemma (Diekmann, 1985). However, dominant males, or males likely to become dominant, may gain disproportionate benefits from these services. In many social species, dominant males obtain the lion's share of reproduction (Kutuskake & Nunn, 2006). Similarly, in cooperatively breeding species, dominant males may benefit from helping young group members because these will grow into helpers for his future offspring. The group augmentation benefits of male services can be translated into other game theory concepts (Bergmuller et al., 2007), such as by-product benefits (Brown, 1983) or pseudo-reciprocity (Connor, 1986). The latter describes investments into by-product benefits: recipients (females, young) use male services in a self-serving way (they survive, grow, get ready to reproduce), which benefits the male as a by-product (anti-predation and territory defence benefits, increased mating opportunities). The key difference to reputation-based partner choice described below is that group augmentation needs neither reputation nor partner choice to function.

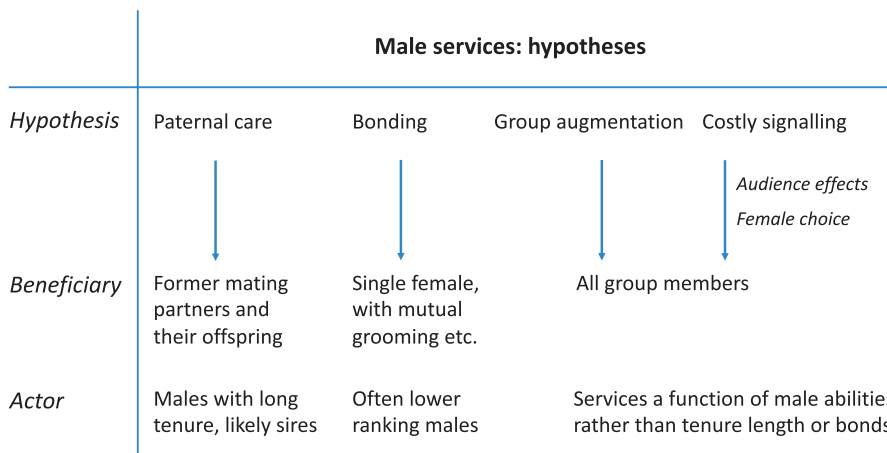


FIGURE 1 Predictions of the four hypotheses considered in this study, focussing on features of both beneficiaries and actors

A final possible explanation is that males are advertising their quality as mates. Theoretical models suggest that unreciprocated services may serve as costly signals of partner quality for future cooperative interactions (Gintis et al., 2001). The crucial features of the concept are that third parties attribute a reputation score to individuals based on their helpfulness and that these third parties choose between potential partners based on this score: the higher the better. Hence, the concept has been termed “reputation-based partner choice” (Sylwester & Roberts, 2013), replacing the initial, potentially confusing term “competitive altruism” (Lotem et al., 2003; Roberts, 1998). We can apply the notion of reputation-based partner choice to females choosing mates and thus to sexual selection. This interpretation has been proposed for primates (Crofoot, 2012; van Schaik & van Noordwijk, 1989; Zuberbühler, 2009), and also for predator approaches in schooling fishes (Dugatkin & Godin, 1992) as well as courtship feeding in birds (Wiggins & Morris, 1986). However, this suggestion was never systematically investigated, perhaps because male services in primates are mostly provided in non-mating contexts, sometimes even in seasons without any mating, which makes it easy to overlook the possibility that they are the product of sexual selection.

Since males may provide various benefits, female preferences for protective males can be expressed during the formation of pair-bonded or single-male groups, and also in polygynandrous mating systems because the reproductive skew produced by male dominance is often incomplete (Kutuskake & Nunn, 2006). In the latter case, female primates may have to remember male services and act on them over extended time periods. This suggestion is not implausible given that females of a bird species, superb fairy wrens, remember to choose those neighbouring males for extra-pair copulation that had moulted into breeding coloration several months before the breeding season started (Dunn & Cockburn, 1999).

Male services in primates may benefit any group member if the function is to signal intrinsic viability (leading to genetic benefits of mate choice to the female) and/or also a male's quality as a parent (leading to additional services once the joint offspring is born) to potential mates. Thus, females would preferentially mate with helpful males because it is self-serving. In conclusion, the concept of reputation-based partner choice (henceforth: costly signalling) predicts that males may provide services as public goods that may vary in frequency or risk depending on their intrinsic quality.

Figure 1 provides an overview of these four possible, mutually compatible explanations for the diverse array of male services and their key predictions for primates or indeed any other lineage that forms stable mixed-sex pairs or stable social groups containing adults of both sexes, thus potentially also birds and some other mammals (see van Schaik & Kappeler, 1997). Because existing studies generally do not provide the necessary information, at this time we are unable to conduct definitive tests of these predictions to establish the relative importance of the hypotheses. Instead, the results section assesses the presence and extent of a male bias in the various anti-predation behaviours through a combination of qualitative review of reports and quantitative analyses where sufficient reports are

available. We also check whether their appearance is not an artefact of confounding variables, such as sexual size dimorphism, substrate or mating system, available for all studies. In the discussion, we will trawl the data for observations relevant to specific predictions, for instance that only likely sires are involved, so as to be able to establish that specific hypotheses cannot explain all the reported cases of male services. There we also consider anti-predation services in birds, other possible forms of male services, as well as the expanding human literature on male services as costly signalling.

2 | MATERIALS AND METHODS

2.1 | Data collection

We conducted a thorough search for publications concerning anti-predation behaviour in wild primates, in which we could quantify the relative participation of each sex. Studies were included in the data set if they (i) described vigilance behaviour, mobbing or a counter-attack in a quantifiable way, (ii) mentioned the predator type (in the case of mobbing and counter-attacking) and (iii) noted the sex of the participants. We had to exclude studies from our quantitative analyses that qualitatively describe a sex bias in the behaviours of interest to us, with statements such as “adult males typically approached the predator most closely, and were more boisterous and more persistent in threatening and following the predator than females” (Rose 1994), or did not sufficiently define the behaviour (Arlet & Isbell [2009] merely mentioned “active defence”).

We limited our search to material published before 2018 (1975–2017). We used the following scientific citation indexing services: Google Scholar, Web of Science, Scielo and PubMed. We also consulted libraries for volumes of *Folia Primatologica* and the *Journal of Anthropology* not available online and the *Primate* volume of the *Handbook of Mammals* (Mittermeier et al., 2013). We further searched the reference lists of each paper included to identify studies that were missed in the initial search. The final list of studies and the data set is given in Table S1.

For anti-predation behaviours, we used the following definitions. Vigilance was defined as an individual visually scanning its surroundings. Reports of vigilance following a predator encounter were excluded, as it is fundamentally different from vigilance in the absence of a predator and is likely to involve different mechanisms and consequences (Caro, 2005). We considered mobbing to be deliberate actions directed towards potential, but non-hunting predators beyond alarm calling (Hartley, 1950; Shields, 1984). We considered a counter-attack to be any active defensive behaviour exhibited in direct response to a predator attack (i.e. attacking, capturing and/or killing an individual). Usually in these cases, a member of the group was in direct interaction with the predator.

For each species included in the sample, we also collected the following variables: average adult male body mass, average adult female body mass, average group size, average group composition, mating system and travel substrate (arboreal or terrestrial), if needed

from various additional references (Braza et al., 1983; Buchanan Smith, 1991; Delson et al., 2000; Ford, 1994; Ford & Davis, 1992; Garber & Teaford, 1986; Gautier-Hion & Gautier, 1976; Gevaerts, 1992; Haltenorth & Diller, 1988; Hernandez-Camacho & Defler, 1985; Mittermeier et al., 2013; Myers et al., 2008; Niemitz et al., 1991; Rodríguez & Boher, 1988; Rowe, 1996; Smith & Jungers, 1997; Sussman, 1991; Wich & Nunn, 2002).

Overall we identified 56 studies that reported 73 quantitative estimates of the following anti-predator behaviours: vigilance, $n = 23$; mobbing, $n = 27$ and counter-attack, $n = 23$ (Table S1). Our sample contained anti-predator behaviour in 45 primate species distributed over 11 families.

Group progressions in open terrain were analysed for various baboon species based on a compilation of studies by Rhine (1986), who divided the moving group in six parts, based on all group members (i.e. including all infants).

2.2 | Sex bias measures

We built indices based on the relative participation of individuals of each sex for each record of anti-predation behaviour (Sex Bias Index, hereafter SBI).

For vigilance, the data presented in the original papers were the percentage of time or samples that individuals spent being vigilant, and we used the average values for each adult sex to calculate the SBI. To create a single value per species that represents the difference between the sexes in vigilance, we first subtracted the female values from the male values ($V_m - V_f$). We then divided this by the total mean vigilance ($SBI_{vig} = \frac{(V_m - V_f)}{[(V_m + V_f)/2]}$).

For mobbing and counter-attacks, we estimated the expected participation for each record of the behaviour of each sex according to the proportion of adult males and adult females in the group composition reported in the study. Where this information was not available in the source study, we used the average group composition for the population (if available), or finally, the average for the species concerned. We then assessed the observed proportion of participation by each sex based on their behaviour during predator encounters. Some studies provided descriptive statements of sex differences in mobbing behaviour rather than quantified observations: either that only one sex consistently engages in mobbing (Harcourt & Stewart, 2007), or that there is no observed difference between the sexes (Cheney et al., 2004). For the former, an observed value of 1 was assigned to the participating sex (and 0 assigned to the non-participating sex); for the latter, each sex was assigned an observed value equivalent to their expected value, resulting in an SBI of 0 (see below). Thus, for mobbing, the observed values (O) were divided by the expected values (E) for each sex ("m": males; "f": females: $X_m = m_O/m_E$ and $X_f = f_O/f_E$). Finally, we subtracted the female value from the male value for the respective behaviour ($SBI_{mob} = X_m - X_f$). The same procedure was used to calculate the SBI_{c-a} for counter-attacks. For the SBI_{prog} in the spatial position in group progressions,

we used the measure of observed versus expected male representation in the front section of the group's progression order, based on the partitioning of the original studies.

For all SBI indices, a value of 0 indicates no difference between the sexes (no bias). Negative numbers indicate a female bias and positive numbers indicate a male bias, with the value reflecting the strength of the deviation from zero. These indices are non-bounded. An index with its limits at -1 and 1 (e.g. $X_m - X_f / (X_m + X_f)$) was not feasible for our analyses, given that the distribution of the resulting values did not allow us to meet model assumptions while controlling for phylogeny.

2.3 | Statistical analyses

To test the patterns of SBIs across primates, we used the software R 3.3.0 (R Core Team, 2016). We first tested whether the SBIs of spatial position, vigilance, mobbing and counter-attacks were significantly different from zero (no bias) or had an overall positive (male bias) or negative (female bias) trend. We carried out phylogenetically controlled (Arnold et al., 2010) generalized linear mixed models with the Monte Carlo Markov Chain (MCMC) technique in the package MCMCglmm (Hadfield, 2010) for all but spatial position. We ran separate null models for each type of behaviour (vigilance, mobbing and counter-attack) using the respective SBI as the response variable.

We also assessed how the mating system influences the sex bias in anti-predator behaviours using the SBI of each behaviour (vigilance, mobbing and counter-attack) as the response variable and the following species-specific explanatory variables in each model: mating system (monogamous, polyandrous, polygynandrous, polygynous), travel substrate (arboreal or terrestrial habits, because this may affect responses: Willems & van Schaik, 2017) and sexual size dimorphism (average adult male body mass divided by average adult female body mass), which could affect the SBI due to a sex difference in risk. Models investigating mobbing and counter-attack behaviour additionally included the predator type (snake, mammal, bird).

To control for possible phylogenetic non-independence, we included a consensus tree (Arnold et al., 2010) of phylogeny as a random effect in all mixed models. The SBIs of mobbing and counter-attacking were transformed by taking the cube root, which fit the model assumptions and does not change the interpretation of the SBI values.

We carried out the MCMC linear mixed models with a burn-in period of 100,000 iterations, for 1,000,000 iterations, and a thinning interval of 900 iterations, with the exception of the null model for counter-attacks, which we ran for 5,500,000 iterations, discarding the first 500,000, with a thinning interval of 5000 interactions, to obtain better mixing of the chains. Our models resulted in acceptable effective sample sizes for all factors (~1000), indicating proper mixing of the model, which was confirmed through inspection of trace plots. Autocorrelations between iterations were acceptably low. We tested specific a priori predictions and thus retained non-significant terms in the models.

3 | RESULTS

3.1 | Spatial positions

An individual's spatial position in a group may reflect its optimal balance of predation risk and access to resources and may thus vary with age, sex and dominance rank (Farine et al., 2017; Janson, 1990). Under normal conditions, that is when perceived predation risk is average and no between-group conflicts are imminent, females tend to lead group progressions (Fichtel et al., 2011). However, this pattern may change when animals perceive an increase in predation risk, when males may take up positions between the group and any approaching predator, a protective spatial behaviour called inter-positioning. Many early studies reported active male inter-positioning (chacma baboons: Hall, 1960; Stoltz & Saayman, 1970); forest baboons: Rowell, 1966; colobus monkeys: Leskes & Acheson, 1970; tanzania monkeys: Kavanagh, 1980). Hall (1967) reports that male patas monkeys actively lead predators away from the group through "a diversionary display." We found no reports of female inter-positioning or diversionary displays.

In open terrain or when crossing dangerous spots, male inter-positioning can also be preventive. DeVore and Washburn (1963) proposed this "adaptive geometry" for baboon groups travelling on the treeless savanna. During group progressions, the two-dimensional structure is squeezed into one dimension, and numerous early studies tested the key predictions, namely a overrepresentation of males at the front of the group, and sometimes also at the rear (Altmann, 1979; Harding, 1977; Rhine, 1975). These positions are mirrored by vigilance patterns (Matsumoto-Oda et al., 2018).

We therefore tested whether the SBI_{prog} at the front of these baboon progressions was well over 0, using a compilation of studies by Rhine (1986), who divided the moving group in six parts. Figure 2a shows this was the case (mean $SBI = 1.01$; if we include two [conservatively] estimated cases: 0.94 ; $t_6 = 7.96$, $p < .001$). There was no significant male bias in the rear part of the group progressions (median $SBI = -0.015$), largely because adult females were also somewhat overrepresented, relative to immatures (Figure 2b). These spatial positions facilitate the male protective behaviours reviewed below.

The only other primates regularly crossing open terrain concern chimpanzees, but the available group progression data concern road crossings, potentially equally dangerous contexts. Detailed studies showed that adult males were significantly more likely than expected to lead (Cibot et al., 2015) or significantly more likely to both lead and make up the rear (Hockings et al., 2006). Males scanned the road more than others and often waited for others. In bonnet macaques, Sugiyama (1971) describes multiple cases when immatures left behind after a group had crossed a road were taken back by different "young adult males" who would occasionally even carry infants on their backs. Moreover, in a striking parallel, human foragers in lion-rich open terrain form progression orders with men in the front and at the rear (Thomas, 2006, p. 236).

Overall, then, there was a consistent male overrepresentation at the front and sometimes the back of these progressions, especially

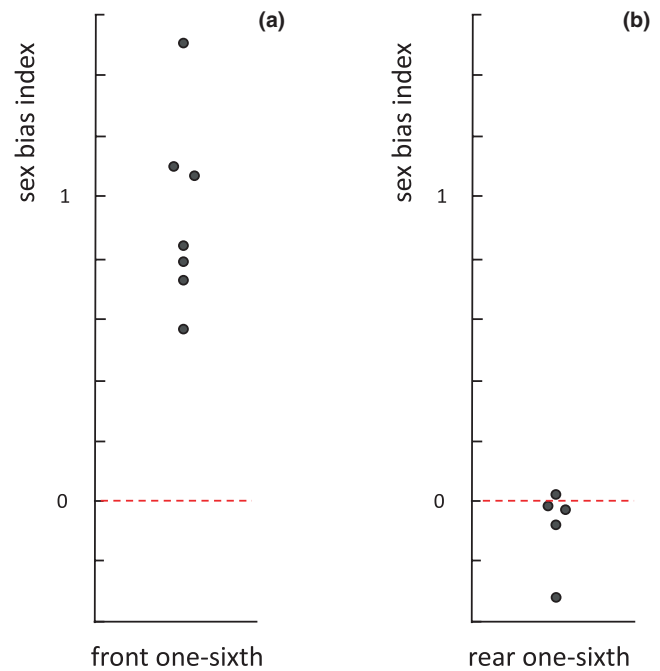


FIGURE 2 The Sex Bias Index (SBI) for position in group progressions in various baboon studies, for both the front one-sixth of the group (a) and the rear one-sixth (b)

in situations of increased risk. Direct observations indicate that these spatial patterns arose due to active choices by males.

3.2 | Vigilance and predator detection

The SBI_{vig} was significantly greater than zero across primates (Table 1), demonstrating that this behaviour is male-biased in the sample as a whole (Figure 3a). Thus, adult male primates were on average more vigilant than adult females, and this sex bias was not affected by travel substrate, mating system or sexual size dimorphism (Table 2). Not enough studies report the identity of individuals detecting predators for a quantitative assessment of the sex bias.

More direct support for male services comes from situations in which males engage in sentinel behaviour, which can be defined as protracted and continuous vigilance at vantage points, usually accompanied by vocal communication (Manser, 1999). Sentinelling is rare among primates. Under natural conditions, it has been described for callitrichid monkeys, the only cooperative breeders among primates, where it is male-biased (Koenig, 1998; Savage et al., 1996). However, where humans hunt monkeys with firearms, males are often recorded as sentinels, in both baboons (Hall, 1960; Maxim & Buettner-Janusch, 1963; Stoltz & Saayman, 1970) and crop-raiding monkeys, where sentinels were "usually adult or subadult males" (Kavanagh, 1980) or the "single breeding male" (Horrocks & Hunte, 1986). Thus, it appears that in species that generally do not rely on sentinels, males can take up sentinel roles in situations of unusual risk. However, it is not known how taxonomically widespread these responses are.

3.3 | Alarm calling

A quantitative analysis of the sex bias in alarm calls was not possible, given that many alarms are false or given to innocuous animals. A sex bias in true alarms may nonetheless be evident. When Hauser and Wrangham (1990) elicited alarm calls by playbacks of eagle calls in three African forest monkey species, “the only adult male present within the group” gave alarm calls in each of them. Even where

TABLE 1 Results of phylogenetically controlled linear mixed models testing if there is a sex bias in the provision of anti-predatory services (SBI) in vigilance ($SBI_{\text{vigilance}}$), mobbing (SBI_{mobbing}) and counter-attack ($SBI_{\text{counter-attack}}$)

	Post mean	Lower 95% CI	Upper 95% CI	p -MCMC
Vigilance – sex bias	0.495	0.164	0.846	.040
Random effect				
Phylogeny	0.038	<0.001	0.221	
Mobbing – sex bias	1.114	0.676	1.560	<.001
Random effect				
Phylogeny	0.011	<0.001	0.041	
Counter-attack – sex bias	0.647	-0.470	1.539	.202
Random effect				
Phylogeny	0.553	<0.001	2.144	

males were not the first, they took over from females in African cercopithece monkeys (Hunkeler et al., 1972; Mehon & Stephan, 2021; Ouattara et al., 2009; Stephan & Zuberbühler, 2016), but also in Asian Thomas' langurs (Wich & de Vries, 2006), upon which males, but not females, would continue to emit alarm calls, often from a prominent position, until the predator had left. Qualitative reports also mention this (e.g. patas monkeys: Hall, 1967; bonnet macaques: Sugiyama, 1971; Phayre's leaf monkeys: Lloyd et al., 2006).

3.4 | Mobbing

The SBI_{mob} was significantly greater than zero (Table 1), demonstrating that these behaviours are male-biased in the sample as a whole (Figure 3b). None of the covariates included in the analysis had a significant effect (Table 3). This pattern is confirmed by various studies that did not make it into the sample because requisite details were missing (e.g. tanzania monkeys: Kavanagh, 1980; white-handed gibbons: Uhde & Sommer, 2002; grey-cheeked mangabeys: Arlet & Isbell, 2009).

3.5 | Counter-attacks

Counter-attacking a hunting predator is the riskiest anti-predator behaviour, and “on the open plains a troop's only protection is the fighting ability of its adult males” (DeVore, 1963). The values for $SBI_{\text{c-a}}$ did not indicate that males generally engage in counter-attacks

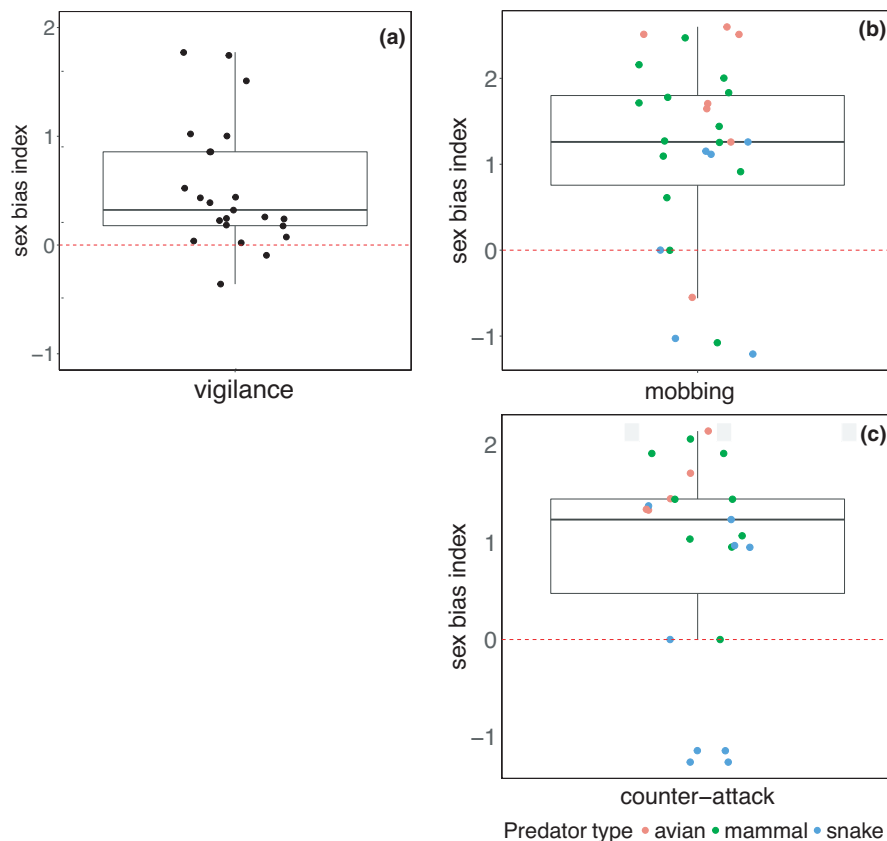


FIGURE 3 Box plot with median and quartiles of the (SBI) for each behaviour analysed (a) vigilance, (b) mobbing and (c) counter-attack. The values on the ordinate represent the SBI (see Section 2) per study, where zero (dashed line) indicates no bias, negative values indicate a female bias, and positive values indicate a male bias. The colour and shape of the points in plots (b) and (c) indicate the different predator types

TABLE 2 Results of phylogenetically controlled linear mixed model comparing the effect of mating system, habitat substrate and sexual size dimorphism on the sex bias (SBI) in vigilance behaviour (SBI_{vig})

Factor	Post mean	Lower 95% CI	Upper 95% CI	p-MCMC
Fixed effects				
Intercept	0.262	-1.184	1.660	.706
Mating system (monogamous vs. polyandrous) ^a	-0.209	-1.649	1.351	.774
Mating system (monogamous vs. polygynandrous) ^a	0.349	-0.716	1.397	.508
Mating system (monogamous vs. polygynous) ^a	0.590	-0.412	1.596	.234
Substrate (arboreal vs. terrestrial) ^a	0.223	-0.491	0.876	.474
Sexual size dimorphism	-0.152	-1.220	0.844	.756
Random effects				
Phylogeny	0.387	0.144	0.728	

^aReference level is the first category in these lists.

TABLE 3 Phylogenetically controlled generalized linear mixed models comparing the effect of mating system, habitat substrate, sexual size dimorphism and predator type on the sex bias (SBI) in mobbing behaviour (SBI_{mob})

Factor	Post mean	Lower 95% CI	Upper 95% CI	p-MCMC
Fixed effects				
Intercept	1.020	-0.546	4.170	.100
Mating system (monogamous vs. polyandrous) ^a	-0.582	-3.179	2.063	.640
Mating system (monogamous vs. polygynandrous) ^a	-0.521	-2.137	1.089	.502
Mating system (monogamous vs. polygynous) ^a	-0.825	-2.205	0.531	.254
Predator type (bird vs. mammal) ^a	-0.494	-1.494	0.745	.324
Predator type (bird vs. snake) ^a	-1.562	-2.953	0.279	.058
Substrate (arboreal vs. terrestrial) ^a	0.199	-1.295	1.422	.760
Sexual size dimorphism	0.129	-1.420	1.667	.858
Random effects				
Phylogeny	0.057	<0.001	0.224	

^aReference level is the first category in these lists.

more than females (Table 1; Figure 3c). However, there was an important interaction effect, because counter-attacks against a bird or a mammal were significantly more male-biased than counter-attacks against snakes (Table 4; Figure 3c). Several other studies not included in the quantitative analysis support this interpretation (Arlet & Isbell, 2009; Eason, 1989; Ouattara et al., 2009), whereas we found no additional cases of female-led counter-attacks. This result also confirms a more limited survey of primate counter-attacks by Willems and van Schaik (2017), which found that males were far more involved than expected, but also noted that counter-attacks on carnivores often involved coordinated behaviour by multiple males, unlike those on other kinds of predators.

Although we did not find that greater size dimorphism indicated a larger male bias in counter-attacks (Table 4), this does not mean that mobbing or counter-attacking predators by males is not risk-free, as illustrated by reports of males getting injured or even killed while defending their group (Arlet & Isbell, 2009). This is also shown indirectly

by the overrepresentation of males in the prey of African crowned hawk eagles (Mitani et al., 2001; Struhsaker & Leakey, 1990), which specializes on forest monkeys. In baboons (Cowlshaw, 1994), males-only coalitions can drive off, and even kill leopards, even though leopards may capture and kill individual adults. In chimpanzees (Boesch, 1991), male-led coalitions can do the same. Thus, even if the risks to males may often be lower than to females, they are far from negligible when it comes to mobbing and especially counter-attacking predators.

4 | DISCUSSION

4.1 | Male anti-predation services

The review yielded evidence of a strong and systematic male bias in anti-predation services. Males were more likely to be at the front of group progressions, especially in contexts of increased risk, were

Factor	Post mean	Lower 95% CI	Upper 95% CI	p-MCMC
Fixed effects				
Intercept	1.804	-0.382	3.964	.109
Mating system (monogamous vs. polyandrous) ^a	-0.711	-3.473	2.202	.600
Mating system (monogamous vs. polygynandrous) ^a	1.275	-0.341	2.952	.120
Mating system (monogamous vs. polygynous) ^a	0.713	-1.232	2.413	.424
Predator type (bird vs. mammal) ^a	0.026	-1.208	1.489	.953
Predator type (bird vs. snake) ^a	-2.587	-2.657	-2.508	<.001
Substrate (arboreal vs. terrestrial) ^a	-0.340	-1.645	1.233	.604
Sexual size dimorphism	0.061	-0.270	0.462	.784
Random effects				
Phylogeny	3.477	1.164	6.879	

^aReference level is the first category in these lists.

more vigilant, sometimes to the point of becoming sentinels, were more active in mobbing and were far more likely to counter-attack felids and monkey-eating raptors than females.

In itself, the sex bias in vigilance provides only weak support for male services. First, vigilance may partly fulfil a social function. In this context, a persistent male bias may merely indicate that they are more likely to be on the alert for male rivals from inside or outside the group that may attack them (Gould et al., 1997). However, the lack of an effect of mating system in the sex bias in vigilance argues against vigilance being exclusively directed at rivals. Second, the male bias may also be caused by males being more peripheral and thus more at risk (Cowlshaw, 1998). In that case, any resulting group-level anti-predation benefits would be a by-product of male self-serving behaviour (see Bshary & Bshary, 2010, for an example of self-serving punishment yielding a public good). Even so, the male bias in vigilance was mirrored by a male bias in mobbing or counter-attacks, which confirms it as a male anti-predation service.

The dependence of the male bias in counter-attacks on the category of predator is not surprising (Crofoot, 2012). Snakes are generally more likely to attack infants and juveniles (Corrêa & Coutinho, 1997; Ferrari & Beltrão-Mendes, 2011; Ferrari & Lopes Ferrari, 1990), and constricting snakes are unlikely to attack additional individuals once they are engaged with prey. The females involved are often the immatures' mothers (Corrêa & Coutinho, 1997; Perry et al., 2003; Quintino & Bicca-Marques, 2013) and probably at the spot when the snake attacked. In contrast, raptors and felids can present a constant danger to all members of the group, as they actively move through the environment, can take large prey and can take multiple victims during an attack.

Overall, these quantitative comparisons reveal a systematic sex bias in anti-predator behaviours in primates. They were found across taxonomic groups and mating systems. In some cases, the differences were so pronounced that we can say males were virtually exclusive providers or at least always took the lead. This was especially true for the riskier behaviours like mobbing or counter-attacks

TABLE 4 Results of linear mixed model comparing the effect of mating system, habitat substrate, sexual size dimorphism and predator type on the sex bias (SBI) in counter-attack behaviour (SBI_{c-a})

against raptors and felids, the latter usually undertaken by male coalitions. Having established their ubiquity and general incidence of male anti-predation services, we can now examine the hypotheses that purport to explain their presence.

4.2 | Male services as parental care

The default assumption concerning male protection against predation is that it represents paternal care. In most primates, male parental care is largely indirect, in the form of protection, rather than direct, as by provisioning or carrying. Because in many studies, the males involved are dominants and have sired infants, our review underscores the importance of this protective role, which was well recognized for the case of infanticide (Palombit, 2015; van Schaik & Kappeler, 1997), but less highlighted for predation avoidance. This shows that the traditional notion that primate males do not engage much in parenting should be replaced by the idea of a sexual division of labour, in which females are more responsible for resources and males more for protection (Mehon & Stephan, 2021). The evident willingness of primate males to provide parental care also matches the observations that primate males can easily be coaxed into direct parenting (Hrdy, 2009) and that likely fathers affect the fitness of their juvenile offspring (e.g. baboons: Huchard et al., 2013) once the latter have cast off their paternity cloak, which makes males unable to recognize their paternity during the period of vulnerability to infanticide (Pagel, 1997).

Sex-specific parenting roles even extend to males in pair-living and thus physically monomorphic species, in line with absence of an effect of mating system on the SBI values. Breeding males lead groups into and out of tree-holes in lion tamarins (Moro-Rios et al. 2018) and are more active in both vigilance and mobbing in marmosets (Ruttenberg, 2005), tamarins (Goldizen, 1989; Savage et al., 1996) and titi monkeys (Dolotovskaya et al., 2019; De Luna et al., 2010). In white-hand gibbons, males are only slightly more vigilant

than females, but “adult males took a more active role in mobbing [pythons, large raptors, tigers] than adult females” (Uhde & Sommer, 2002). Thus, even in monomorphic species, including some in which males provide direct care by carrying young, this sexual division of labour in predation avoidance can be observed.

The pattern among sexually monomorphic primates suggests that a similar division of labour can also be found in birds, despite the strong tendency towards biparental provisioning. The few available studies (Cunha et al., 2017; Regelmann & Curio, 1986; Sternalski & Bretagnolle, 2010) strongly support this view.

Despite the great importance of parental care, this review shows that it cannot be the sole explanation of male anti-predation services, because in many cases males without offspring provide these services too. First, in various species, newly immigrated males provide protection services when they could not have sired any offspring in the group (e.g. vervet monkeys: Baldellou & Henzi, 1992; mountain gorillas: Yamagiwa, 2001; tufted capuchins: Wheeler, 2008; diana monkeys: Stephan & Zuberbühler, 2016; anubis baboons: Matsumoto-Oda et al., 2018). Second, males may protect adult individuals, which could not have been sired by males currently present in the group (gelada baboons: Iwamoto et al., 1996). Third, males of all ranks sometimes participate about equally in anti-predation behaviours, also in species in which male mating success is generally skewed (e.g. ring-tailed lemurs: Bolt et al., 2015; olive baboons: Paciência et al., 2017). Fourth, the riskiest forms of anti-predation behaviour, counter-attacks aimed at hunting predators, also involve the participation of non-sires. In one case, a white-faced capuchin male played a major role in wresting a juvenile from a snake, even though the victim was born well before he entered the group (Jack et al., 2020). Other counter-attacks involve many males (Boesch, 1991; Cowlshaw, 1994), and it is unlikely these males had all sired offspring, let alone done so equally. The same holds true for the protective positioning in baboons and chimpanzees by males in general.

In sum, we have enough instances to suggest that these behaviours are not solely performed by male parents, although the available literature generally lacks data on relatedness and more targeted studies are needed to assess whether male categories within a group differ in their tendency to provide protective services.

4.3 | Male services and social bonds

One alternative explanation was that males provide their services towards their bonded partners and their offspring (not necessarily the males'). Although this may explain some cases, social bonds are found only in a modest number of species and also cannot explain the majority of anti-predation services, because they generate public goods, as the benefits often accrue to all group members. Thus, alarms, as a consequence of sex-biased vigilance and detection, will inform all group members in the vicinity. Mobbing, likewise, produces a public benefit, given its well-documented function of discouraging the predator attacking in the future (Caro, 2005). Only counter-attacks could be selectively targeted at helping bonded females or their young, but

in many cases, these are joint attacks where multiple males participate. Moreover, it is clear in many cases reviewed above that the males that provided the services did not have social bond partners, as where basically all adult males participate or where young or recently immigrated males provide the services.

In some species, it is difficult to exclude the possibility that males provide services to non-bonded females as an investment into establishing social bonds. However, as males entertain strong social bonds with only one or few females, explanations invoking public benefits (costly signalling or group augmentation) are more parsimonious. Similarly parsimonious is the explanation that some males do favour bonded partners because they fathered their offspring. We therefore conclude that even if services may favour bonded partners, they do not do so exclusively, and if they do, it may often be due to other processes.

4.4 | Male services and group augmentation

So far, we have shown that neither the parental care nor the social bonding hypothesis furnishes a full explanation of male services. In many cases, a male or the males cannot select who the beneficiary is, and often the benefit is public. Such cases are consistent with group augmentation. This phenomenon is often not considered because most models on public goods assume the logic of an N-player prisoner's dilemma, where contributions are maladaptive. However, non-linear benefit functions of investment yield negative frequency-dependent selection, that is coexistence between contributions and failure to contribute (Archetti, 2009). Conflicts over contributions can be further reduced as males that are, or will soon be, reproductively successful benefit disproportionately from their contributions, providing them with a net benefit (see also Nunn & Lewis, 2001).

Conversely, however, male reproductive skew is often concave, with dominants taking disproportionate amounts. This would predict that males that have only poor chances of becoming dominant should refrain from providing these services, especially where the main benefit of male services are through improved growth and survival of offspring. This prediction remains to be tested, but we gained from the review that all males of all species have a tendency to provide protective services, regardless of career prospects. Second, in very large groups, the skew becomes weak (van Schaik et al., 2004). We would therefore expect such services to be far less pronounced, if present at all, in species living in large groups, such as baboons or some macaques. This prediction is not consistent with the available data, however.

Future work is needed to test the importance of group augmentation. For now, although we cannot reject group augmentation as the major functional benefit of male services, we think that more specific benefits might provide a better explanation.

4.5 | Male services as costly signalling

The final hypothesis considered here is that male services may also represent a costly signal of a male's genetic quality and parenting

ability, which arose because females select their mates at least in part based on this costly signal. We found various observations consistent with this view (see Figure 1), such as the fact that males also provide anti-predation services if they are not sires, appear to have a general tendency towards boldness in the face of predators, and also deliver services when not in social bonds with particular females. Likewise, maturing males were observed to provide services during adolescence, often before dispersal. For instance, subadult males participate in male-biased mobbing (red titi monkeys: De Luna et al., 2010) or protective inter-positioning (savanna baboons: Rhine et al., 1981; chimpanzees: Cibot et al., 2015). This suggests a causal link to sexual maturation rather than paternity (cf. Zuberbühler, 2009), which leads to the prediction that castrated males should reduce their services or even stop providing them altogether. An experiment by Gyger et al. (1988) with roosters revealed that castrated males continued to make food calls but stopped alarm calling at raptors.

Consistency with the costly signalling hypothesis does not amount to critical support, because these observations might also be compatible with group augmentation, although the latter is less specific in its predictions (see Figure 1). Although the available studies provide indications, these do not amount to definitive tests. One strong prediction is that females should prefer to mate with males providing costly services. Arseneau et al. (2015; see also Arseneau-Robar et al., 2016) presented correlational data for vervet monkeys in the context of males helping females in between-group contests. A weaker version that pertains directly to anti-predation services is that females have a preference to associate with service-providing males, with increased mating access as a by-product. Several observations suggest that such a preference exists in some species. Female wild black spider monkeys only remained at sites where the calls of harpy eagles had just been played back when adult males were present (Symington, 1987). Likewise, chimpanzee females only crossed open savanna to go to another forest patch when males were present (Tutin et al., 1983). Data from birds provide more direct support for the prediction: female fowl mate more with roosters that give more alarm calls (Wilson et al., 2008) and female grey partridges prefer vigilant males as mates (Dahlgren, 1990).

Another critical prediction is that a larger female audience should lead to more or more risky male services. Again, our review could not test this, but Cunha et al. (2017) found such an audience effect for mobbing in various species of monogamous birds.

In conclusion, the costly signalling hypothesis is promising, as it is compatible with the male parental care hypothesis and the social bonding hypothesis, with the first representing the likely ancestral state and the second an expression of alternative male reproductive tactics. Although it lacks critical support among primates for now, investing in targeted studies is warranted.

The costly signalling hypothesis is strengthened by its compatibility with sexual selection. A female preferring male services may harvest three types of fitness benefits. First, the services immediately provide immediate direct fitness benefits to females associating with males, which females should develop a preference for. Second, the females may acquire delayed direct fitness benefits in that the same males, having sired offspring, will provide above-average male parental care, either

as protectors (mainly in primates) or as providers (mainly in birds). Third, to the extent that the services are costly and reflect intrinsic viability, a preference for them provides genetic benefits (also called “indirect” benefits) to females. This mix of direct and genetic benefits may explain why spectacular male-only ornaments are absent in most of the species with male services. Ornaments act as costly signals of intrinsic male viability (Andersson, 1994), but provide females relying on them to select mates only with genetic benefits (and may also produce trade-offs in species with male parental care when they reduce a male's ability to provide parental care relative to their absence: Kokko, 1998). Accordingly, ornaments are especially pronounced in lekking species, in which males are not associated with females beyond the mating context and thus also not involved in rearing the young (Cuervo & Møller, 1999).

Another argument in favour is that the same costly signalling interpretation is increasingly offered for male services in humans. In our species, male services in the form of protection and food provisioning may have been crucial in the evolution of our hunter-gatherer foraging niche. Beyond male protection against predation, men also compete to be generous providers (Hawkes & Bliege Bird, 2002) and may focus on large shareable prey rather than energetically more efficient smaller prey because this allows them to share widely (Hawkes, 1991; but see Wood & Hill, 2000). Indeed, people of both sexes prefer to live in the same camp as good hunters (Marlowe, 2010), whose generosity may bring them higher reproductive success through extra-pair mating or assortative partner choice (Smith, 2004). Thus, both protective and generous men gain prestige (Friedl, 1978), which may translate into fitness benefits, being preferred as partners by women with the highest reproductive potential, or better treatment of their children (Hawkes, 1991; Hill & Hurtado, 1996). Even after the establishment of food production, men initially continued to compete through redistributive feasts (Harris, 1977), that is through generosity rather than through exclusion (Flannery & Marcus, 2012).

Recent experimental work links male services in humans to reputation-based female choice: in the presence of a female audience, men contribute more to charity (Iredale et al., 2008) or are more generous in public goods games (Tognetti et al., 2016; Van Vugt & Iredale, 2013) than when alone or observed by men only. In a direct experimental test of competitive altruism they donated more to an attractive female fundraiser, especially when responding to a donation by another man (Raihani & Smith, 2015).

5 | CONCLUSION AND OUTLOOK

Male services are a general phenomenon in primates and hence warrant a functional explanation. We discussed four possible explanations: paternal investment, maintenance of mixed-sex social bonds, group augmentation benefits and costly signalling of quality in a mating market. Distinguishing between these non-exclusive hypotheses requires targeted observational and experimental studies of males with known dispersal and reproductive histories. We propose that future work should focus primarily on testing predictions of the costly signalling hypothesis, because these tests will simultaneously reveal the potential merits of the other three hypotheses. Many

of its predictions can be tested directly: females should prefer the proximity to males providing protective services over those that do not; females should prefer to mate with males in proportion to the combined frequency and costliness of their services; male services should also be delivered by newly immigrant males; they should be more pronounced in species in which females can exert more and more immediate mate choice (as in multi-male groups or birds with extensive extra-pair copulations, year-long pair bonds or breeding in colonies); they should be more pronounced when the female audience is larger; they should emerge during adolescence and disappear when males are castrated or suffer large drops in testosterone; and they should be most pronounced in species with greater opportunities (high risk of predation and males abilities to defend or opportunities for provisioning). We look forward to observational and experimental studies that conduct tests of these predictions.

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CONFLICT OF INTEREST

We declare no conflicts of interest.

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