



## Review Article

## The evolution of between-sex bonds in primates

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## ARTICLE INFO

## Keywords:

Male-female affiliation  
Friendship  
Power  
Monopolisation potential  
Nonhuman primates  
Human pair-bond

## ABSTRACT

Social bonds can be a way for individuals to gain access to crucial resources and services that cannot be taken by force and are therefore subject to leverage. Bonds between the sexes can provide access to services that are specific to the other sex. Females exert leverage over males in terms of mating access, males have leverage over females in terms of the service protection, and both sexes exert leverage over the other sex in terms of tolerance and agonistic support. While mating access can be coerced in some circumstances, most services cannot be forced. Here, we use theoretical considerations to explore when sources of leverage over the opposite sex lead to between-sex bonds. Focussing on primates living in multi-male multi-female groups, we predict that leverage over the other sex will be higher, when 1) the receiver benefits on average more than the provider, 2) receivers cannot share the resource, and 3) the resource is rare and valuable. If these conditions are fulfilled, and given the mutual nature of a social bond, we expect bonds to be found, 4) when long-term targeting of the same partner yields benefits. We argue that a female's main source of leverage is mating access, whereas males mainly exert leverage over females in terms of protection of females and offspring. The combination of female mate choice with male protection and care for young is expected to promote between-sex bonds; reduced female cohesion and/or secondary female dispersal are expected to further increase the strength of between-sex bonds. The investment in shared offspring results in interdependency between male and female strategies, but the different services provided by females and males indicate that affiliative exchanges associated with bonds between the sexes will be typically asymmetric and vary over time. Thus, bonds between the sexes are expected to form in a limited number of circumstances where both sexes have leverage over the other sex in terms of their respective sex-specific services. While a systematic test of this proposal is hampered by the dearth of data on species lacking social bonds between the sexes, the data currently available are consistent with our hypothesis.

## 1. Introduction

Stable affiliative relationships between the sexes within a larger multi-male multi-female (or multifamily-) group are a core element of

human societies and intricately linked to a suite of characters including sexual division of labour, male provisioning of females during reproductively costly phases, and direct male care for infants (Alexander & Noonan, 1979; Chapais, 2008, 2013; Quinlan & Quinlan, 2008; van

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Schaik, 2016). Nonhuman primates living in multi-male multifemale groups, while not showing this complete suite of traits, resemble humans, yet differ from many non-primate group-living mammals in the common occurrence of between-sex affiliative relationships that transcend the period of mating activity (Palombit, 2010; Rosenbaum & Silk, 2022; Smuts, 1985). To understand the evolutionary drivers responsible for the formation of differentiated stable affiliative relationships between the sexes, here referred to as between-sex bonds (BSBs), it is necessary to identify the benefits that both sexes reap from the relationship.

Evidence is accumulating for adaptive benefits of social bonds in terms of increased survival and/or reproductive success (Ostner & Schülke, 2018; Snyder-Mackler et al., 2020; Thompson, 2019) for female-female (Kajokaite, Whalen, Koster, & Perry, 2020; Silk et al., 2010), male-male (Schülke, Bhagavatula, Vigilant, & Ostner, 2010), and also for between-sex bonds (Archie, Tung, Clark, Altmann, & Alberts, 2014). Conceptual frameworks based on socioecological theory exist for the evolution of female-female and male-male social bonds. Specifically, the formation of female social bonds has been explained by the nepotistic benefits females can gain from cooperating with kin under specific socioecological scenarios (Sterck, Watts, & van Schaik, 1997; van Schaik, 1989). The evolution of affiliative bonds between males is predicted under medium to low male monopolisation potential, when bonded males benefit from a reliable partnership by supporting each other in political within-group coalitions (Ostner & Schülke, 2014; van Hooff & van Schaik, 1994). Currently, we lack a similar framework for the evolution of social bonds between the sexes.

In this paper, we develop and discuss a testable conceptual framework proposing which conditions favour the evolution of between-sex bonds in primates. Primates living in multi-male multi-female groups lend themselves to the study of between-sex bonds given the permanent presence of both sexes for extended periods of time outside the mating period, the detailed knowledge on individual social behaviour available for many species, and the information from long-term studies on wild populations with known individuals on demographic processes and fitness outcomes (Kappeler & Watts, 2012). We start by identifying the effect of resources coveted by either sex on within and between-sex bond formation. Next, we argue that bonds evolve to access resources that are prone to leverage (cf. Lewis, 2002, 2018) and propose under which conditions bonds are expected. We deduce whether these sex-specific sources of leverage will actually give rise to between-sex bonds and describe available empirical evidence. Building on our conclusions, we identify three potential, not mutually exclusive, settings that predict when between-sex bonds are more likely to be found in multi-male multi-female primate groups. We do not attempt a complete review on within-group between-sex bonds in primates or a formal test of our idea, but instead aim to draw a conceptual roadmap for future research.

## 2. Bonds within and between the sexes

Consistent with others (Massen, Sterck, & de Vos, 2010; Ostner & Schülke, 2018; Silk, 2002; Thompson, 2019) we define social bonds (sometimes also called ‘friendships’ or ‘good relationships’) as strong (compared to the average affiliative relationship in a given group), equitable, and stable affiliative relationships between two individuals consistent with definitions of human friendship (Blieszner & Roberto, 2004; Wrzus, Zimmermann, Mund, & Neyer, 2017). Despite the requirement of stability, bonds are inherently dynamic as they build on the give and take in the relationship; otherwise they would fall apart. Yet, they gain stability over time because individuals, the environment they live in, and the market conditions initially change rather slowly, and thus partners become interdependent (Hinde, 1976).

Bonds among females, among males, and between the sexes differ due to different pre-conditions. First, the sexes compete over different resources (Emlen & Oring, 1977; Wrangham, 1980), which in turn differ in their degree of shareability. It is easier for females to form same-sex

bonds than it is for males, because females primarily compete for resources shareable with some others (food), whereas males mainly compete for non-shareable resources (fertilizations), making it easier for females to share and bond compared to males (van Hooff & van Schaik, 1992, 1994). Second, the sexes differ in the resources they covet (see above) and may only have similar interests in specific conditions (Wrangham, 1980). Consequently, bond formation among females is expected in many situations (Sterck et al., 1997; van Schaik, 1989). Social bonds among males are expected only when male monopolisation potential is relatively low, and consequently bonded, cooperative males outcompete non-bonded non-sharing males, i.e. via cooperative rank attainment (Ostner & Schülke, 2014). Male-female bonding is most likely when the interests of the male and female partner are aligned (Rosenbaum & Silk, 2022) and – as we will argue – when it leads to interdependence, e.g. when it concerns the survival of mutual offspring. Therefore, we expect that services that benefit mutual offspring will be particularly likely to generate between-sex bonds.

Increased equitability of give and take between partners, a defining trait of social bonds, may be more easily achieved in a same-sex than in a between-sex relationship (Haunhorst, Schülke, & Ostner, 2016). The expected lower degree of equitability of exchange between the sexes originates both from (a) inequality in resource holding potential between the sexes, with males being the more dominant sex in the majority of nonhuman primates (Davidian, Surbeck, Lukas, Kappeler, & Huchard, 2022; Lewis, 2018), and (b) sex-differential needs and offered resources, consequently affecting different potential commodities to be traded and benefits to be reaped from between-sex bonds (Haunhorst et al., 2016). In developing this framework, we first take the perspective of either sex separately to evaluate the resources to be offered, and only subsequently, merge both perspectives, and argue that only when both interests converge, we expect to find social bonds as defined above.

Note that we are interested in the evolution of differentiated stable between-sex affiliative relationships in groups composed of several adult males and females (Chapais, 2013; van Schaik, 2016). Only in these groups, differentiation, and thus partner choice, by both the female and the male is possible. We do not discuss the evolution of social monogamy or the development of pair-bonds in pair-living or cooperatively breeding nonhuman primates. Phylogenetic reconstruction indicates that pair-living in mammals evolved from an ancestral state of solitary females with male care as a consequence and not a cause of pair-living (e.g., Kappeler & Pozzi, 2019; Lukas & Clutton-Brock, 2013). We also do not include affiliative relationships between related males and females, such as the bonds between bonobo mothers and their adult sons (e.g. Surbeck, Mundry, & Hohmann, 2011). However, we include examples from one-male multi-female systems, because patterns can be instructive, and differentiation in the distribution of male-to-female affiliation is possible, as is variation among females in their preference for the only male. However, between-sex-bonding in the strict sense, namely differentiation from both sides, is by definition impossible in these cases. Nevertheless, in several of the species that typically form one-male multi-female groups, occasionally groups with more than one male are formed that may be informative on the potential for female differentiation among males in these species.

Between-sex bonds of various time depths have been reported in a number of multi-male multi-female primate species in all major primate radiations (Fig. 1). Examples include red-fronted and ring-tailed lemurs (Gould, 1996; Ostner & Kappeler, 1999; Pereira & McGlynn, 1997), vervet monkeys (Young, McFarland, Barrett, & Henzi, 2017), two species of capuchin monkeys (Perry, 2012; Tiddi, Aureli, Schino, & Voelkl, 2011), baboons (Altmann, 1980; Huchard et al., 2010; Lemasson, Palombit, & Jubin, 2008; Moscovicic et al., 2010; Nguyen, Van Horn, Alberts, & Altmann, 2009; Palombit, Seyfarth, & Cheney, 1997; Smuts, 1985; Städele et al., 2019), macaques (Haunhorst et al., 2016; Massen & Sterck, 2013) and African great apes, including chimpanzees (Langergraber, Mitani, Watts, & Vigilant, 2013; but see, Machanda, Gilby, & Wrangham, 2013) and bonobos (Stevens, de Groot, & Staes,



**Fig. 1.** Between-sex bonds have been reported in a range of primate species with a multi-male multi-female social organisation. From top left to bottom right: female (left, with infant) and male red-fronted lemur at Kirindy Forest, Madagascar (photo: J. Ostner); grooming session between a male and female chimpanzee showing closeness with face to face mutual grooming at Tai National Park, Ivory Coast (photo: L. Samuni); female Assamese macaque grooming a male at Phu Khieo Wildlife Sanctuary, Thailand (photo: K. Srithorn); alpha male and female white-faced capuchin forming a coalition at the Lomas Barbudal Monkey Project, Costa Rica (photo: S. Perry).

2015). Based on the available data we cannot ensure that these relationships are built and maintained from both sides of the partnership, as most studies cited here present undirected data. Yet, given that these relationships are often stable over time and across reproductive seasons (even if sex-differential investment patterns may fluctuate from one season to the next), we assume at least a certain degree of investment into the relationship from both partners. While the taxonomic distribution of species exhibiting BSBs points to obvious gaps in our knowledge and calls for a phylogenetic targeting of e.g. lemurs, Atelines, and African and Asian Colobines, it seems safe to say that BSBs are taxonomically widespread in primate species with multi-male multi-female groups.

### 3. Power: The role of leverage in between-sex bonds

The fitness benefits of social bonds suggest that, next to dominance relationships, bonds have evolved to gain access to resources, but the power exerted through dominance relationships or through social bonds differ. Following Lewis (2018, 2002), we distinguish two distinct ways in which power can be expressed, namely through dominance, i.e. the ability to coerce access to a resource by force, and through leverage, i.e. the ownership over an inalienable resource that another individual is granted access to. Dominance is particularly effective in excluding others from material resources, such as food and mating partners; if a resource can be obtained by force, social bonds are not needed and are not expected to evolve. In contrast, leverage exists when a resource cannot be obtained forcefully by dominants (Lewis, 2002). The

individual providing access to a resource, i.e. the provider, has leverage over the receiver when the provider can offer a valuable service that the receiver desires but cannot take by force. Such resources include the service of providing access to inalienable goods such as fertilizable eggs (mating access), or services that concern behaviour such as protection, tolerance for access to food, or cooperation in coalition formation. While mating access can also be taken by force, e.g. coerced mating, the latter type needs the cooperation of the provider. Thus, resources can be controlled either via dominance or via leverage. While male primates are considered to exert power mainly through dominance, female primates often exert power through leverage (Lewis, 2018, 2002). Yet, this sex difference does not exclude that females can exert power through dominance or that males have leverage through services they provide. The difference between dominance and leverage becomes evident, for example, when females associating with a high-ranking male enjoy beneficial access to material resources (food: Heesen, Rogahn, MacDonald, Ostner, & Schülke, 2014) or when individuals that are exclusively able to provide experimentally induced access to food, temporally receive more grooming (Fruteau, Voelkl, van Damme, & Noe, 2009), in both cases without an associated change in dominance rank.

Following from the above, the behavioural interactions paving the way to access the resource also differ between the two power categories, dominance and leverage. Since dominance is linked to physical force, dominance-controlled resources are obtained via aggression or the threat of aggression (Davidian et al., 2022). Instead, leverage entails providing access to a service without being forced and is facilitated by (short-term) affiliative behaviour, such as grooming, or, long-term, by

the formation of a bond. While bonds can serve multiple functions (Thompson, 2019), we explore the evolution of bonds and consider the transactional nature of social interactions leading to bonds. We predict bonds to evolve in order to gain access to resources that are under the power of leverage (Vermande & Sterck, 2020).

An individual who has leverage over another individual in terms of a desired service it can provide is expected to be the affiliation-receiving individual in exchange for providing the service. For example, when females have leverage over services coveted by males, we expect affiliation to be initiated and maintained by males, whereas when males have leverage over services desired by females, we expect affiliation to be initiated and maintained by females. To identify this difference, we distinguish between mainly male interest in the relationship (male to female affiliation) and mainly female interest in the relationship (female to male affiliation). Only when both sexes show mutual interest in the relationship, it qualifies as a social bond (between-sex bond, BSB).

An exchange of affiliation for a service is expected under several conditions. First, providing a service should on average in the short-term be less beneficial to the individual providing it than for the receiving individual. When the service benefits the provider more than the receiver, the providing individual will bestow the service irrespective of the behaviour or the bond with the receiver (as a by-product of its own interest). The provider only exerts leverage when the receiver benefits more. Second, the provided services should be valuable to the receiver and be relatively rare, such as suggested in Biological Market Theory (Noë & Hammerstein, 1994, 1995). A service with value that is relatively scarce will benefit its receiver. Note that within the framework of the evolution of bonds, we consider affiliation a commodity that can be traded, and as such serves as payment for access to a more limited service, not as a service in itself. Third, the resources or services should be targeted at a specific individual, e.g. to the bond partner, and not be a widely shareable service provided to many or all group members at the same time. Since the provider can choose who receives the scarce service, the receiver obtains either the service or nothing. For the receiver, while the value of a service is important, it is even more important to obtain the service at all. These three conditions predict short-term exchanges of affiliation. They can also explain social bonds when, additionally, the long-term targeting of the same partner yields benefits. Thus, fourth, bonds are formed when they yield benefits due to long-term selecting of the same partner, such as a) when benefits are delayed (e.g. grooming is given repeatedly by the same individual and only sporadically interchanged by this partner with agonistic support (Schino, 2007)), b) when benefits increase in the long run (e.g. when cooperation is better among well-known and trusted or predictable individuals), c) when individuals mutually depend on each other (e.g. are related or share parental care), d) when providing the service to individuals others than the primary partner results in opportunity costs (e.g., preventing the bond partner from seeking others), or e) when the obtained benefit at any one moment is small and only accumulates over time. Note that these conditions are not mutually exclusive and apply to both within- and between-sex bonds. Here we focus on between-sex sources of leverage.

Testing whether between-sex bonds (BSBs) are formed under the predicted conditions requires data on the presence or absence of BSBs in species that vary in the indicated variables. However, typically only data on the presence of BSBs are available, while an absence of publications on BSBs in a particular species does not guarantee that BSBs are absent (i.e., a file drawer effect). Also, data linking directional affiliation to sources of leverage are rare, e.g. while there are studies showing the association of BSBs and mating success or male agonistic support, fewer studies link resulting mating success to male-biased affiliation or male support towards females to female-biased affiliation (for references see below). Our aim is to present a conceptual framework and investigate whether available data on between-sex behaviour are consistent with the predicted patterns.

#### 4. Female sources of leverage and consequences for male to female affiliation

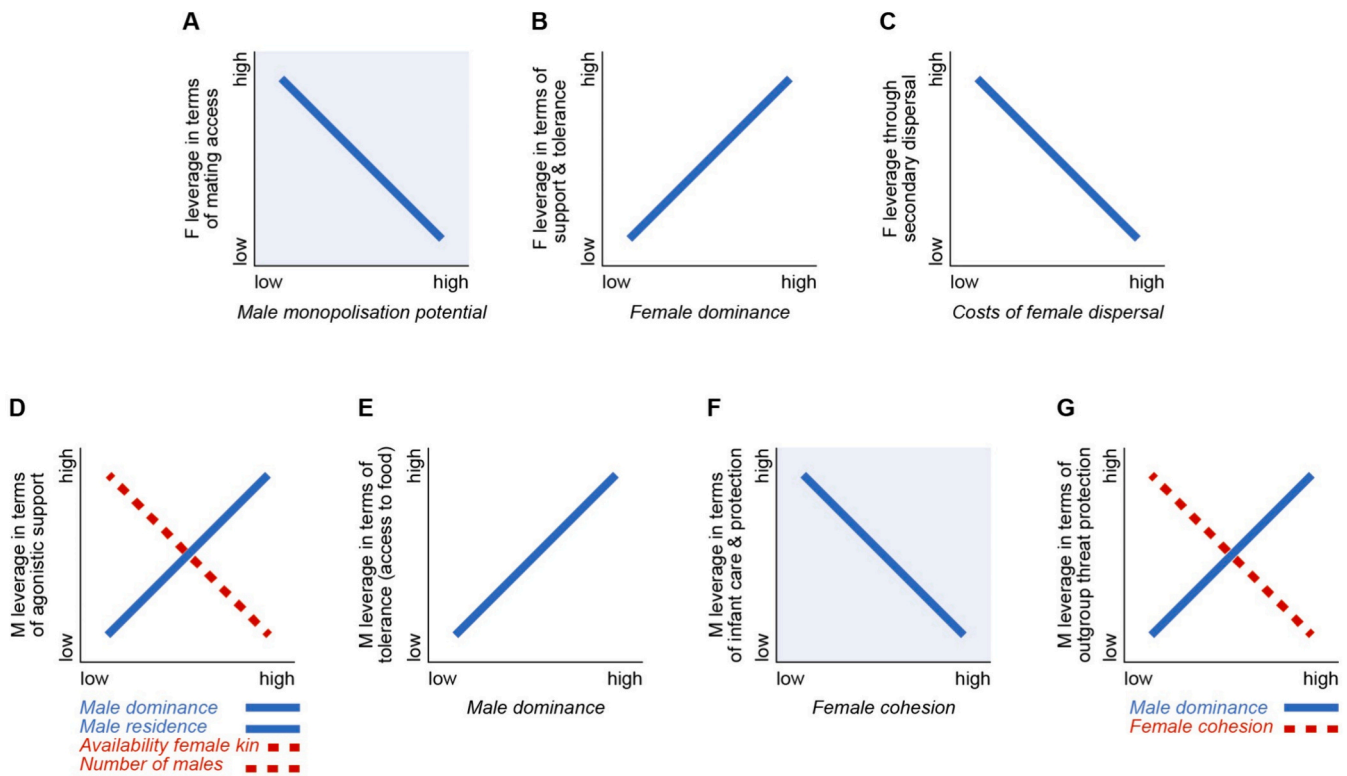
Females can exert leverage over males in terms of various services, namely 1) mating access, 2) agonistic support, 3) tolerance for access to food, and 4) female group membership mediated by female secondary dispersal (Table 1). However, males may coerce females to mate and thus achieve fertilization through dominance, reducing female leverage over males in terms of mating access. We distinguish between the main sources of leverage females have over males and the different moderators affecting their strength of leverage, and deduce for each of these services, when differentiated male to female affiliation is expected. We explore whether the available literature supports or opposes our expectations.

##### 1) Mating access

Mating access is a female service that provides males with a crucial resource through female choice (Emlen & Oring, 1977; Wrangham, 1980), namely the possibility to father offspring. This gives females leverage over males (Lewis, 2002), and female mate choice is an expression of this leverage. Males restrict female mate choice (and thus leverage) when they coerce a female to mate, or display strict mate guarding and restrict other males' access to a female through male-male competition (Davidian et al., 2022; Muller, Kahlenberg, & Wrangham, 2009; Smuts & Smuts, 1993). Reversely, this predicts increased female mate choice when males' ability to monopolise females is lower

**Table 1**  
Sex-differential sources of leverage, ways to exert leverage, and factors moderating leverage.

	Female source of leverage	Way to exert leverage	Moderators: female leverage high when
1	Mating access	Female mate choice (countered by male coercion)	Male monopolisation potential low, approximated as low paternity skew, low male-biased sexual dimorphism
2	Female agonistic support	Refuse support	Female more powerful (as sex class or individual)
3	Tolerance for access to food	Refuse access to food	Female more powerful (as sex class or individual)
4	Female group membership mediated by secondary dispersal	Female threatens to disperse	Costs of female secondary dispersal low, e.g. alternative groups around, immigration easy
	Male source of leverage	Way to exert leverage	Moderators: male leverage high when
1	Male agonistic support within group	Refuse support	Male more powerful (as sex class or individual); male group residence long; number of female kin low; number of males low
2	Tolerance for access to food	Refuse access to resource	Male more powerful (as sex class or individual)
3	Male infant care and protection	Refuse protection	Risk for infant high (e.g. infanticide); female with infants less cohesive or in subgroups; male more powerful (as sex class or individual); male group residence long
4a	Male protection against predators and other groups (resource defence)	Refuse protection	Male larger than female; females less cohesive or in subgroups
4b	Male protection against other groups (defence of females)	Male benefit: no male leverage	Not expected



**Fig. 2.** Sex-specific sources of leverage and factors determining their strength, upper panel A-C: female leverage over males, lower panel D-G: male leverage over females. Shaded graphs indicate the main sources of leverage a sex has over the other (see Table 1 and text for details).

(Fig. 2A). The monopolisation potential decreases with increasing female estrous synchrony and/or number of rival males (Gogarten & Koenig, 2013; Ostner, Nunn, & Schülke, 2008), and less clearly signaled female fertility (Nunn, 1999). The degree of monopolisation potential can be approximated as the skew in male reproductive success (Ostner et al., 2008) and also as male-biased sexual dimorphism in body or canine size (Cassini, 2020). In order to test whether female's leverage over males in terms of male mating access leads to male to female affiliation, we need data across primates on the degree of male monopolisation potential or a proxy thereof (male reproductive skew, sexual dimorphism), together with dyadic data on directed male to female affiliative behaviour and its effect on male mating access.

Few studies have investigated whether male-biased grooming resulted in enhanced mating success for males. Males appear to trade grooming for matings for example in long-tailed (Gumert, 2007) and rhesus macaques (Massen et al., 2012) and in a community of wild East African chimpanzees characterized by a shallow hierarchy, and, thus, potentially reduced male monopolisation potential (Kaburu & Newton-Fisher, 2015). In other cases, mostly characterized by high male power differentials, males groomed females less than they were groomed by them (regardless of reproductive season or female fertility) and male grooming propensity was not predicted by female fertility: male mating success was predicted by male dominance rank and not by male grooming of females (chacma baboons, Clarke, Halliday, Barrett, & Henzi, 2010; Eastern chimpanzees, Kaburu & Newton-Fisher, 2015; redfronted lemurs, Port, Clough, & Kappeler, 2009; Japanese macaques, Soltis, Mitsunaga, Shimizu, Yanagihara, & Nozaki, 1997). While far from conclusive, patterns of male to female affiliation are consistent with a reduced male monopolisation potential and increased female leverage over mating access.

Another piece of evidence comes from the association of between-sex affiliative relationships and mating or paternity success in a number of species. However, as these analyses often used undirected data, we cannot investigate a potential sex-differential bias in the maintenance of

these relationships. In rhesus (Kulik, Muniz, Mundry, & Widdig, 2012; Massen et al., 2012) and Assamese macaques (Ostner, Vigilant, Bhagavatula, Franz, & Schülke, 2013), chimpanzees (Langergraber et al., 2013), and olive baboons (Städle et al., 2019; Städle, Vigilant, Strum, & Silk, 2021) bidirectional affiliation or spatial association with a female predicted a male's mating or reproductive success independently of his dominance rank. All of these species are characterized by low to intermediate male reproductive skew (Ostner & Schülke, 2014; Städle et al., 2019; Sukmak, Wajjwalku, Ostner, & Schülke, 2014). However, in chacma (Weingrill, 2000) and yellow baboons (Nguyen et al., 2009), both characterized by much higher male monopolisation potential, male-female affiliative relationships, while present, did not enhance a male's chance of subsequent matings. These patterns also, while not suitable to test our idea, are consistent with the prediction that males may use affiliation to increase mating success in situations where females can exert mate choice.

## 2) Agonistic support

Females may provide males with agonistic support, yet often females are more reluctant than males to engage in a fight and thus provide less value in this respect (Lewis, 2018). If females support males in within-group conflicts, their support is most effective when the supporter adds substantial power to the coalition (Noë, 1992), i.e. when the supporter is physically strong or holds important positions, i.e. are high-ranking (Fig. 2B). This suggests that male to female affiliation for female agonistic support is found in species where females (as a sex class) are dominant over or larger than males or between males and high-ranking females in non-female dominant species. While there is more variation in intersexual power differentials than previously thought, males are still the dominant sex in the majority of primates outside lemurs (Lewis, 2018). Therefore, male to female affiliative relationships aimed at gaining female support are not expected to be widespread.

Support for these predictions is expected in lemurs as the taxon with

widespread obligate female dominance (Lewis, 2018), or in co-dominant species. We found no evidence for female agonistic interventions on behalf of males in lemurs, and thus no female leverage in terms of this service. In co-dominant bonobos, females support of males is observed, yet is limited to their adult sons, enhancing their sons' dominance and mating success, and is not shown towards unrelated males (Surbeck et al., 2011) and thus again not a source of leverage. Male and female dominance positions are interspaced in co-dominant vervet monkeys (Hemelrijk, Wubs, Gort, Botting, & van de Waal, 2020; Young et al., 2017), making this species another candidate for female leverage over males in terms of agonistic support. Indeed, males with more and more central female partners achieve higher dominance rank, but female agonistic support is rare (4 % of male-male conflicts) and has no effect on male dominance trajectories (Young et al., 2017), speaking against female leverage in terms of this service. In capuchin monkeys female agonistic support of males has been proposed to be relevant during male rank upheavals or to maintain alpha male status (Perry & Manson, 2008; Tiddi, Aureli, Schino, & Voelkl, 2011). However, as the support is directed towards the alpha male who has a high paternity probability with all females in his group, supporting him and extending his tenure is in the females' own interest, reducing female leverage over males.

Females may also support males on the between-group level when aiding to keep rival males from immigrating. White-faced capuchin females actively support the alpha male in fending off extra-group males trying to enter the group (Gros-Louis, Perry, & Manson, 2003; Perry, 2012; Perry & Manson, 2008). While less powerful than males in terms of strength and weaponry, females are valuable allies given their long-term residence in the group and hence their long-term availability as allies (Perry, 2012). As infanticide by new alpha males is the main cause of infant mortality and hence a major driver of female lifetime reproductive success in white-faced capuchins (Fedigan, 2003; Perry, 2012), all resident females and the alpha male converge in this interest of maintaining group stability. Due to this joint interest in keeping incoming males out, females have no leverage over this service and we do not expect differentiated male to female affiliation for agonistic support between groups. Overall, agonistic support as a source of female leverage over males, while conceivable, does not seem to be convincingly realized in nonhuman primates and thus does not explain male to female affiliation in primates.

### 3) Tolerance for access to food

Another service that females can provide to males is access to monopolised resources, such as food. Food is not the main limiting resource for males' fitness, but males clearly need to feed, especially if they are larger than females. If resources are monopolisable, dominant individuals have increased access to those scarce resources. They can be tolerant in the sense that they refrain from exercising their monopolisation potential towards specific individuals, which gives them leverage. Thus, the conditions under which females can provide this benefit to males converges with the settings outlined above in the case of female agonistic support of males: females have more leverage over males in terms of providing access to resources when they are dominant or larger than males (Fig. 2B). If males are dominant over females, females are less able to provide access and males are likely able to access their required nutritional resources by themselves. Thus, there is only a narrow range of species where we would expect this source of leverage to be important. Perhaps unsurprisingly, we found no evidence in the literature for female leverage over males due to female tolerance of males in the feeding context.

### 4) Female group membership mediated by female secondary dispersal

In primates, female group membership is crucial for male mating opportunities, since most matings occur within groups (Alberts, 2012; Ostner et al., 2008). In female-dispersal species (Koenig & Borries,

2012), females exert leverage over both resident and extra-group males with respect to group membership, in particular when females show secondary dispersal, i.e. subsequent migration following the first dispersal away from the natal group. Nulliparous females (prior to natal dispersal) will have little leverage due a lack of interest of resident males in mating with these (potentially) related females. In addition, while nulliparous females have leverage over extra-group males whose group they enter, when dispersal only happens once, dispersal-related leverage diminishes once settled in the new group. In contrast, female leverage in terms of group membership is high in species with secondary female dispersal, particularly when costs of secondary dispersal are low (in terms of leaving, joining, or forming a new group; Fig. 2C). Dispersal costs will be relatively high when females are accompanied by dependent offspring, since a dispersing infant is vulnerable to male infanticide in a new group.

Although a strong potential source of female leverage, secondary female dispersal is relatively rare among primates (Furuichi, Yamagiwa, & Aureli, 2015; Sterck & Korstjens, 2000) and is basically absent in female-dispersing species living in multi-male multi-female groups (spider monkeys, Riveros, Schaffner, & Aureli, 2017; bonobos and chimpanzees, Schubert et al., 2011; woolly monkeys, Stevenson, Zárate, Ramírez, & Heneo-Díaz, 2015; muriquis, Strier, Possamai, & Mendes, 2015) (but see red colobus Starin, 1991). Consistent with the relative lack of female secondary dispersal in primate multi-male groups, we did not find evidence for this type of female leverage over males. In contrast to multi-male multi-female groups, female secondary dispersal occurs regularly in one-male multi-female systems; thus, data on male affiliation to females in these species is informative. We expect resident males to use affiliation to keep females in their group. While the sole male in a one-male group is expected to direct affiliation to all (unrelated) females, leading to undifferentiated male to female affiliative behaviour, there may also be a bias towards those females that are most likely to disperse, such as parous females without a dependent offspring (mountain gorillas, Harcourt, 1979; lowland gorillas, Manguette et al., 2020; Thomas langurs Sterck, Willems, Van Hooff, & Wich, 2005; review, Sterck & Korstjens, 2000), who have the highest leverage over the male in terms of dispersal. In one-male multi-male groups, evidence argues against differentiated male grooming depending on female reproductive state (mountain gorillas, Habumuremyi, Deschner, Fawcett, & Robbins, 2018) or relevant analyses are lacking (mountain gorillas, Rosenbaum, Hirwa, Silk, Vigilant, & Stoinski, 2016). In temporary two-male situations in mountain gorillas, males tended to be more often responsible for seeking proximity to fertile than non-fertile females (mountain gorillas, Sicotte, 1994), yet variation in initiating proximity between the different males to specific females was not mentioned. Altogether, data are lacking for a conclusive treatment of the link between female secondary dispersal and differentiated male to female affiliation.

#### 4.1. When do we expect differentiated male to female affiliation?

Differentiated male to female directed affiliation in multi-male multi-female groups is expected in a limited number of settings. First and foremost, mating access is the main source of female leverage over males and is only realized when male monopolisation potential is low. If power differentials between males are very high, females will be monopolised and will not be able to show mating preferences. The few data we found in this respect are consistent with this idea, but systematic tests are needed. Second, given the distribution of intersexual physical power in primates, agonistic support and female-granted access to resources will rarely result in male to female affiliation. Third, repeated secondary female dispersal constitutes theoretically a strong source of female leverage, but it is rarely found in species with multi-male multi-female groups and thus will rarely lead to differentiated male to female affiliation. Overall, the main source of female leverage in primates that can lead to male affiliation towards females is females providing males

with mating access and, thus, female mate choice.

## 5. Male sources of leverage and consequences for differentiated female to male affiliation

Males can provide several services that lead to male leverage over females, including 1) agonistic support within the group; 2) tolerance for access to food; 3) infant care, including protection from infanticide; and 4) protection from predators or outgroup conspecifics (Table 1). As these are all behavioural services, female coercion to access male sources of leverage over females is not possible. We distinguish between the main sources of leverage males have over females and the different moderators affecting the strength of leverage, and deduce when differentiated female to male affiliation is expected. We explore whether the available literature supports or opposes our expectations.

### 1) Agonistic support

Males can support females in within-group conflicts against other males or females. Supporting a female against another male, the supporting male can benefit directly, for example during the mating season when support keeps rivals away from females, while at other times there may be no direct benefit, thus creating male leverage over females. Supporting a female against other females in conflicts over access to resources or to strengthen her dominance position becomes particularly important in non-female-nepotistic species, where females can rely less on kin support (Chapais, 1995), and consequently the availability of female kin decreases a male's leverage over females in terms of agonistic support (Fig. 2D). The value of support (Kummer, 1978), and thus male leverage, also increases when support is more beneficial, i.e. when a male has more power due to a higher dominance rank or physical strength, and when support is more predictable for a female, for which a male's residence time in a group is a proxy (Fig. 2D). Finally, if male support is important, males have less leverage when there are many males available (Fig. 2D). Note that we propose selective pressures that lead to female to male affiliation and are not concerned with the occurrence of male support for female partners once a BSB has formed.

Evidence linking female to male affiliation and male agonistic support comes from multi-male multi-female groups of capuchin monkeys and several cercopithecines: in tufted and white-faced capuchin monkeys, adult females maintain the strongest relationships with the alpha male, direct most grooming to him, and receive most support in conflicts from him (Di Bitetti, 1997; Perry, 1997; Tiddi, Aureli, Schino, & Voelkl, 2011). In Assamese (Haunhorst, Heesen, Ostner, & Schülke, 2017) and rhesus macaques (Kulik et al., 2012), as well as in chacma (Moscovice et al., 2010) and olive baboons (Lemasson et al., 2008), males supported females more when their affiliative relationship with this female was stronger. Indeed, in these species it is also usually the female that grooms the male more than vice versa (Haunhorst et al., 2016). Similarly, in a mountain gorilla group with temporarily two males, each male provided support for the female that preferentially associated and groomed him (Watts, 1992). After one of the males disappeared, the sole silverback no longer biased his support (Watts, 1992). Thus, while not being a proper test of our prediction, these data are consistent with females directing affiliation to a male in exchange for male agonistic support.

### 2) Tolerance for access to food

A male may refrain from exercising his monopolisation potential and instead provide feeding tolerance to females, resulting in improved access to food for the female enjoying the tolerance. A male's ability to provide tolerance (and thus his leverage over females) depends on his monopolisation potential, with higher ranking males having more leverage and consequently receiving more affiliation from females (Fig. 2E).

Indeed, female grooming of males and/or overall affiliative relationship strength predicted tolerance in feeding trees, time spent co-feeding with the male partner, or female feeding efficiency in several species (Guinea baboons, Goffe & Fischer, 2016; Assamese macaques, Haunhorst et al., 2017; tufted capuchin monkeys, Janson, 1985; Tiddi, Aureli, Polizzi Di Sorrentino, Janson, & Schino, 2011; Tiddi, Aureli, Schino, & Voelkl, 2011; mountain gorillas, Watts, 1992).

### 3) Infant care and protection

Given the high costs of parental care for mammalian females, male participation likely constitutes a valuable service and thus can be a source of male leverage over females. Primate females, as any mammal, provide most care for infants (Kleiman & Malcolm, 1981), yet allomaternal care by other individuals, including males, is regularly found (Mitani & Watts, 1997; Ross & MacLarnon, 2000). Males provide care, either in the form of carrying and provisioning or in the form of infant protection, preferentially to their genetic offspring or to infants for which paternity probability is high (Smuts, 1985; van Schaik & Paul, 1996). Direct male care, i.e. carrying and provisioning of infants, is rare among primates, taxonomically mainly restricted to monogamous (or polyandrous) Callitrichidae and Cebidae (reviews: Dunbar, 1995; Fernandez-Duque, Vallengia, & Mendoza, 2009; Goldizen, 1990), and infrequent in multi-male multi-female species, thus likely not an essential source of leverage of males over females. By contrast, male protection against infanticidal males is a crucial source of leverage in many primate species given the almost universal threat of infanticide in nonhuman primates (van Schaik, 2000). Protection becomes increasingly important in species with high infanticide risk (Hrdy, 1979; van Schaik, 2000). Thus, male leverage in terms of infant care is higher when infanticide risk is higher (van Schaik, 2000), when male protection cannot be shared because females with dependent offspring are spatially less cohesive, and when a male can provide better paternal services, by being dominant and better at protecting, or long-term resident and thus more predictable to females (Fig. 2F). We predict that under these conditions females with infants seek the protective proximity of males and expect that female to male affiliation correlates with the degree of male care for the female's offspring.

Male Hanuman langurs and white faced capuchins protect infants against potentially infanticidal males (Borries, Launhardt, Epplen, Epplen, & Winkler, 1999; Perry & Manson, 2008) and yellow baboons and Assamese macaques support infants in within-group conflicts (Buchan, Alberts, Silk, & Altmann, 2003; Minge, Berghänel, Schülke, & Ostner, 2016) (but see Kulik et al., 2012). As expected, females with dependent infants actively seek the proximity of males both in one-male (mountain gorillas, Harcourt, 1979; Rosenbaum et al., 2016) and multi-male groups (chacma baboons, Palombit et al., 1997). In other species, affiliative relationships between males and females (based on undirected data) predict male association with the females' infants (Assamese macaques, Ostner et al., 2013) and protection of infants against harassment (yellow baboons, Nguyen et al., 2009). While this later evidence is consistent with affiliation linking to male protection, the directionality of affiliation remains to be determined.

### 4) Male protection against predators or outgroup conspecifics

Males can protect females against two types of out-group threats, namely predation and between group conflicts (see Table 1, source of leverage 4). During between group conflicts males can engage as "hired guns" in resource defence or ward off competitors in female defence (Bshary, Richter, & van Schaik, 2022; Teichroeb, 2022). Males are better at detecting predators when they spend more time than females monitoring the environment for competing males (white-faced capuchins, Rose, 1994; Thomas langurs, Steenbeek, Piek, van Buul, & van Hooff, 1999) and as a result detect threats sooner than females. In addition, they are usually stronger or less vulnerable and thus better equipped to

protect. Vigilance and protective behaviour are both services to females. Females may entice a male to protect (through grooming or mating, Bshary et al., 2022), but the benefits of detecting predators or defending resources are shared by all group members when groups are small or cohesive. When females are less cohesive or subgroups are formed, they may associate differentially with more alert or protective males (Bshary et al., 2022), leading to male leverage in terms of protection (Fig. 2G). Male protection will be especially valuable when males are larger than females, thereby increasing a male's leverage over females (Fig. 2G). When the benefits of defence against extra-group competitors are shared among males, i.e. when takeovers are prevented (female defence), males themselves gain from this service, there is no male leverage, and hence female to male affiliation is not expected. When, however, subordinate males are vital for defending against extra group males or for preventing take-overs, but the benefits of group stability fall disproportionately on a few or only the alpha male due to high reproductive skew, as seen in red-fronted lemurs and white-faced capuchins (Fedigan & Jack, 2011, 2004; Muniz et al., 2010; Ostner & Kappeler, 2004; Port, Johnstone, & Kappeler, 2010), females should incentivize subordinate males via affiliation (Perry, 1996, 2012).

Short-term female to male affiliation affected male between-group conflict participation in wild vervet monkeys, as female grooming enhanced a male's probability to participate in a subsequent between-group conflict (Arseneau-Robar et al., 2016). This study also provided evidence that punishment or coercion may provide access to a source of leverage, since females also aggressed against non-participating males, which led to an increase in subsequent between-group activity of the punished males (Arseneau-Robar et al., 2016). This seems to contradict the argument that services cannot be coercively obtained. However, a punished male has the option to refuse to support a female and, on several occasions, did so in the vervet monkey study. Altogether, empirical data highlighting the processes by which females obtain male protection against out-group threats are scarce.

5.1. When do we expect differentiated female to male affiliation?

Like male to female affiliation, female affiliation directed to males is only expected in a limited number of settings. First, female affiliation can serve to receive male agonistic support or tolerance for access to food. Yet evidence is weak and, alternatively, males can simply grant their preferred female support or access to food once the between-sex bond is in place. Second, male care in the form of protection against infanticide is likely a strong source of male leverage over females, and males in some species bias their protection towards infants of those females they share a close relationship with, but more data on directed behaviour are needed to conclusively test the link between affiliation and infant care. Third, female to male affiliation can serve to receive male support and protection against infanticidal and predatory threats from outside the group, in particular when groups are large or dispersed, yet data to support this proposition are rare. Altogether, in primates the main source of male leverage that leads to female to male affiliation is expected to be male protection of herself and her offspring. Note that this key male service to females is linked to the key female service to males, namely mating access.

6. The evolution of between-sex bonds in primate multi-male multi-female groups

Social bonds between the sexes are expected when both males and females have an interest in this relationship with the other sex, i.e. when both sexes can exert some leverage over the other sex (Fig. 3). When exploring a one-sided perspective on affiliation for a service, the main source of leverage a female has over males is granting mating access, while a main source of male leverage is care and protection of infants and their mothers. Thus, a mutual interest emerges with respect to reproduction and investment in mutual offspring. These sex-specific sources of leverage are most important in groups with low male

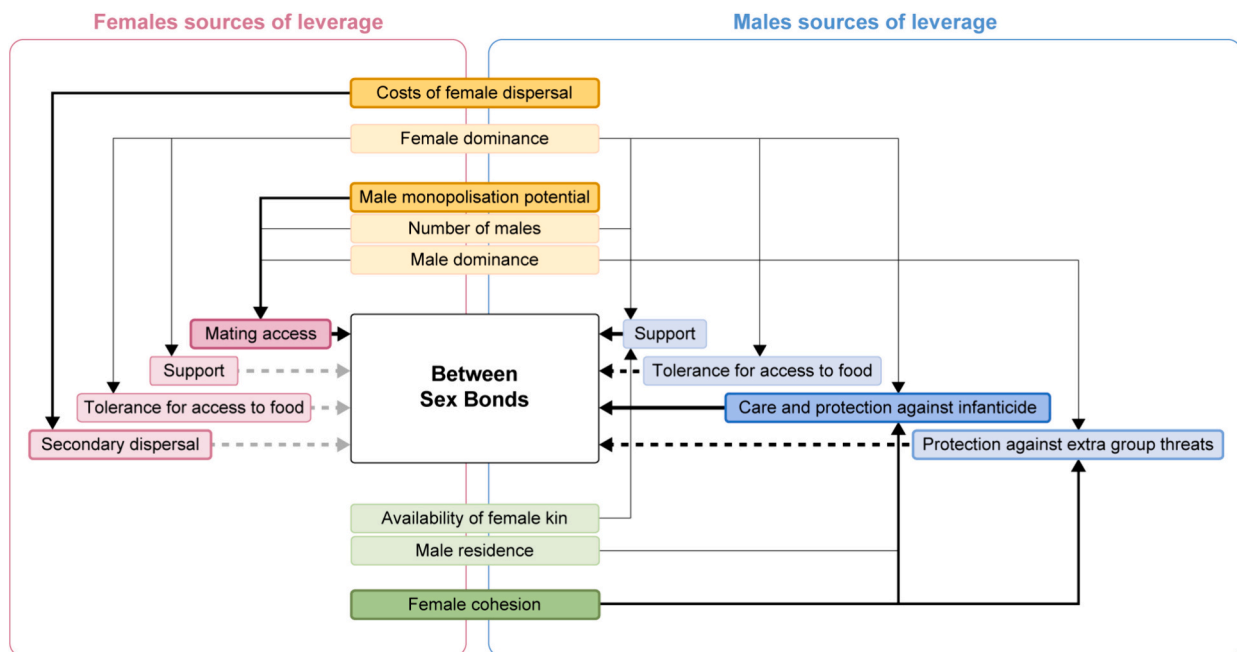


Fig. 3. Factors giving rise to between-sex bonds by influencing the sources of leverage one sex has over the other. Sources of female leverage over males in red, i.e. mating access, agonistic support, tolerance for access to food, and female group membership mediated by female secondary dispersal. Sources of male leverage over females in blue, i.e. agonistic support, tolerance for access to food, infant care, including protection from infanticide, and male protection from predators or outgroup conspecifics. More important sources of leverage are given in darker colours. Factors influencing predominantly female leverage in yellow, male leverage in green (more important factors in darker colours); note that some factors affect both sexes' leverage, e.g. female dominance over males. Connection between factors affecting sources of leverage (thick black lines: strongest effect; thin black lines: potential effect) and between sources of leverage and the occurrence of between-sex bonds (thick black arrows: strongest effect; dashed arrows: intermediate; grey dashed arrows: only rarely realized). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



monopolisation potential, when male sexual coercion of females is not feasible and offspring require protection. In such groups, BSBs are expected.

We propose three non-independent settings that can lead to BSBs in primates living in multi-male multi-female groups, starting from 1) female mate choice combined with male protection of offspring; 2) the components from 1 combined with low female cohesion; and 3) the components from 1 combined with female secondary dispersal. Common to all three settings is the interplay of female choice of her mating partners in relation with the mutual need for male care of infants. First, the main route to BSBs is found when female mate choice and male care for offspring coincide. When female mate choice for a specific male is combined with the need for male care and protection of the infant, e.g. due to high risk of infanticide or predation, a mutual interest in the resulting offspring, or fitness interdependency, results. This requires that a male's residency in the group is long enough to allow him to care for the infant. We, thus, predict the presence of BSBs to be more likely in situations of reduced male monopolisation potential in combination with male care for offspring, as seen for example in some macaque and baboon species with reduced alpha male paternity concentration and male residency in the group long enough to provide care to own offspring (Haunhorst, Fürtbauer, Schülke, & Ostner, 2020; Städele et al., 2021).

Second, if on top of female choice and male care for young there also is low female cohesion, this affects the degree of male leverage in protecting females and offspring. Female cohesion can range from compact groups, to dispersed groups, to temporary subgroups for parts of the day, to more or less permanent subgroups that meet regularly (cf. fission-fusion: Aureli et al., 2008). In species where females are less cohesive, either because they generally have a large group spread or because they form subgroups for part of the day(s), associating with a protector male is more valuable for females and their offspring than in more compact groups (Bshary et al., 2022; van Schaik & Kappeler, 1997). In addition, lower cohesion of females reduces male monopolisation potential and thus increases the degree of female choice and her leverage over fertilizations. Thus, when females are less cohesive, bonds are expected to occur more frequently and to be more exclusive. Whereas in a cohesive group females can share a male protector, in less cohesive groups the need for each female (and her infant) to have her own male caregiver is greater. This can lead to increased female competition for male partners and assortment by dominance rank in BSBs (Baniel, Cowlishaw, & Huchard, 2018; Haunhorst et al., 2020).

In a more extreme version of low female cohesion, relatively stable subgroups of females are formed. A male monopolises such a subgroup, leading to stable one-male units within a larger multi-male multi-female group, also called multilevel systems (Grueter et al., 2020). If the association between a specific male and female is due to male physical power and monopolisation of the female subgroup, thereby restricting the females' mate choice (e.g. "female transfer by males" as seen in hamadryas baboons, Swedell et al., 2011), it is not considered a BSB. In contrast, if the association between a specific male and female results from combined female mate choice and male care, it is regarded a BSB, for example when secondary dispersal of females is common (see below; e.g. in Guinea baboons, Goffe, Zinner, & Fischer, 2016). Thus, BSBs based on mutual female and male leverage are only expected in multilevel systems in certain situations.

Third, if female choice and male care co-occur with secondary female dispersal, female leverage is increased. However, this setting will be rare, since secondary female dispersal is relatively uncommon among primates and concentrated mainly in species exhibiting one-male multi-female groups instead of in multi-male multi-female groups where BSBs can develop (Furuichi et al., 2015; Sterck & Korstjens, 2000). The potential explanatory value of this setting in addressing female-male relationships and, in particular, BSBs in female dispersal species remains to be explored. Variation in BSBs in multi-level societies forms a good starting point, since some of these species exhibit secondary female

dispersal (hamadryas baboons: Sigg, Stolba, Abegglen, & Dasser, 1982; Swedell et al., 2011; Guinea baboons: Goffe et al., 2016).

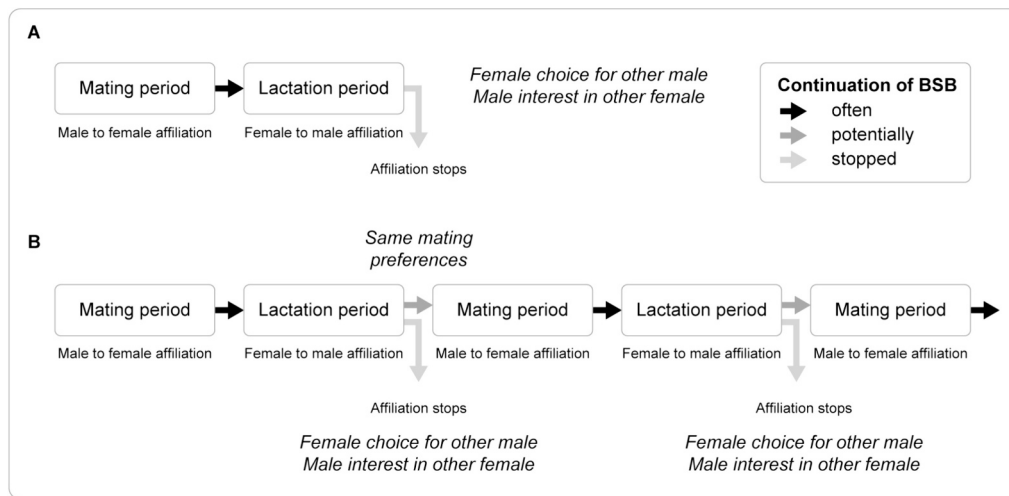
## 7. Temporal characteristics of between-sex bonds

BSBs are expected to have specific temporal characteristics concerning their symmetry. The exchange of affiliation in between-sex bonds will be less symmetric compared to same sex partners, due to differences in resource holding potential between the sexes. Indeed, in many species, females groom males more than vice versa (Haunhorst et al., 2016; Palombit et al., 1997; Watts, 1992; Weingrill, 2000). Yet, we expect this pattern to change predictably over time, depending on the variation in the degree of leverage each sex has, with female leverage over males peaking during the mating period and male leverage over females during the lactation period, i.e. the period of infant dependency. Consistent with this, in several species, males groom (long-tailed macaques, Gumert, 2007; rhesus macaques, Massen et al., 2012) or approach (chacma baboons, Baniel, Cowlishaw, & Huchard, 2016) more during the mating season, potentially to secure mating access, while females groom and approach more when males provide care for their infants (Palombit et al., 1997), potentially to secure male protection.

In a temporal sequence, the BSB will start when a male secures increased mating access through male affiliative behaviour towards the female. Male affiliation (and male care for the female's current infant) directs female mate choice, thereby increasing the male's subsequent mating success (Seyfarth, 1978; Smuts, 1985). Following female parturition, the direction of affiliation reverses and turns into female to male affiliation to ensure male care and protection for herself and offspring (Fig. 4a). This between-sex relationship may end when the infant is sufficiently independent and the female no longer requires male investment (Palombit et al., 1997), since at this point in time both the male and female re-evaluate their mate choice options (Fig. 4A). In particular, the relationship ends when the male disperses or when the probability to fertilize a particular female a second time is low. Consistent with this, short term between-sex relationships terminated at infant independence, infant death, or at female cycle resumption have been found in different populations of chacma baboons (Baniel et al., 2016; Moscovice et al., 2010; Palombit et al., 1997), where male group residence is relatively short (Palombit et al., 1997) or where male dominance ranks change quickly (Baniel et al., 2016).

As for settings where males have a chance to fertilize the same female repeatedly ("repeat paternities", Rosenbaum & Silk, 2022), long-term BSBs will be found. We specifically expect positive feedback leading to long-term BSBs if (1) male group residence is long enough to allow for repeated conceptive cycles with the same female, (2) male monopolisation potential is low enough to ensure that male partners will be able to sire offspring (and not all access is monopolised by the dominant male), and (3) females have a certain degree of mate choice (Ostner et al., 2013). In situations with long male group residence (modal male group residence > interbirth interval), female to male affiliation for male care and protection will last until the female is fertile again, leading to a subsequent period of male to female affiliation to obtain mating access (Fig. 4B). The increased paternity probability of the bonded male will then direct his behaviour and will lead to a positive feedback and interdependency.

Such long-lasting BSBs encompassing more than one mating and subsequent lactation period are found in several species of macaques and baboons (Haunhorst et al., 2016; Massen & Sterck, 2013; Ostner et al., 2013; Städele et al., 2019, 2021) and – based on association data – in chimpanzees (Langergraber et al., 2013). In this situation, the market-driven transactional nature of affiliation may be replaced by an emotionally-based mechanism of relationship maintenance ("emotional book-keeping", Schino & Aureli, 2009). All these species are characterized by relatively low reproductive skew (Ostner et al., 2008), and 'repeat paternities' of the same female and male have been reported (Rosenbaum & Silk, 2022), making the continued investment in the



**Fig. 4.** Temporal patterns in between-sex bonds (BSBs): a) short term BSBs are not continued after the lactation period; and b) fitness interdependencies may arise if mating privileges lead to increased paternity probability and thus a common interest in infant care, facilitating long term BSBs spanning several reproductive events.

relationship worthwhile for both sexes. These studies produce evidence for more stable between-sex relationships due to a feedback loop between female mate choice and paternal care (Ostner et al., 2013). This fitness interdependence has been identified as an important driver of cooperation across animals when the outcome of individuals' behaviour influences each other's fitness (Aktipis et al., 2018; Roberts, 2005). A critical evaluation of this proposal requires more data on species representing the range of male reproductive skew, female mate choice and male group residence length.

## 8. Between-sex bonding in humans

Human societies are characterized by between-sex pairs living within larger groups. Identifying the drivers of BSBs in multi-male multi-female groups of nonhuman primates can therefore inform us about the evolution of pair living in humans (Chapais, 2013; van Schaik, 2016). However, the degree of mating exclusivity within a bonded pair differs between humans and nonhuman primates. Whereas in humans mating, and consequently paternity, is typically concentrated in the pair partner (for reviews see Anderson, 2006; Larmuseau, Matthijs, & Wenseleers, 2016) (Belgium, Larmuseau et al., 2013; UK, Sykes & Irvén, 2000; but see Asia, Balaesque et al., 2015; Ireland, Moore, McEvoy, Cape, Simms, & Bradley, 2006), sexual relationships in group-living nonhuman primates are usually not limited to the social bond partner (rhesus macaques, Massen et al., 2012; chacma baboons, Moscovice et al., 2010). In fact, in nonhuman primates, female promiscuity actually enhances a female's chance of having a male bond partner during the lactation period when males have a short group residence (Moscovice et al., 2010).

Hypotheses for the evolution of human pair living focus either on male dominance leading to male mate guarding of females (Coxworth, Kim, McQueen, & Hawkes, 2015) or on male leverage over females due to male provisioning of offspring (Hawkes, 2006; Kaplan, Gurven, Winking, Hooper, & Stieglitz, 2010; Kaplan, Hill, Lancaster, & Hurtado, 2000; Marlowe, 2003). Our perspective adds that human pair living results from mutual partner choice mediated by female leverage over males through mating access and male leverage over females through infant care and protection. This allows predictions to be made about the settings and dynamics of human BSBs.

Human pair living is affected by the human-specific life history, particularly the extended period of immature development. This extended offspring dependency on care beyond the interbirth interval to the next infant enhances mutual dependency and long-lasting bonds. At the same time, it affects the negotiation between pair partners, as the

female need for male care and provisioning is increased and hence is male leverage. Females can counter this dependency on male provisioning by recruiting care from other sources such as their family, often their own mothers (Strassmann & Garrard, 2011), or building on their own resources (MacDonald & Dildar, 2018) (but see Amri, Adnan, & Fitri, 2022). In humans, patterns of between-sex associations are diverse, and evaluating the evidence would require a separate review. In such a review, the first step would be to determine the nature of human between-sex associations: do they represent "true" BSBs based on mutual female and male preferences; or are they between-sex associations based on male dominance? The role of male dominance versus mutual preferences can be measured at a societal, i.e. cultural, or individual level. The variation of human between-sex associations ranging from those based on male coercive power to BSBs represent an ideal test ground for our hypotheses on the effect of female mate choice and male care for offspring on the emergence of BSBs.

## 9. Summary

In this review, we invoked the concept of power and its two distinct sources, dominance and leverage, as drivers of the absence or presence of differentiated stable affiliative relationships, or social bonds, between the sexes in nonhuman primates living in multi-male multi-female groups. We identified services that can potentially be exchanged between the sexes and explored whether these resulted in leverage for either sex's perspective separately. We consider female leverage over males in terms of mating access and male leverage over females in terms of protection of females and their offspring to be the strongest sources of leverage. We then merged both sexes' perspectives to identify three settings that facilitate the evolution of between-sex bonds (BSBs) by increasing leverage on both sides. Overall, BSBs within multi-male multi-female groups are expected in a limited range of settings, namely under intermediate to low male monopolisation potential. We found mostly evidence in favour of BSBs, yet research to confirm the absence of BSBs is needed. Only a more complete assessment of the conditions leading to the absence or presence of BSBs will allow a critical evaluation of our proposal. The sources of leverage that promote BSBs in primates may also apply to human pair bonds, adding a driver for human pair-living in addition to male mate guarding and male parental investment. This perspective also gives women agency, which is missing from the other two hypotheses. In sum, the relationships between the sexes can be built either on male dominance (cf. Davidian et al., 2022), or on the interplay of mutual female and male leverage resulting in BSBs.

## 10. Future research

Systematic data on the occurrence and temporal dynamics of between-sex bonding are needed, along with data on the proposed predictors, such as male reproductive skew, male group residence length, kin patterns, and female spatial cohesion. Future work, particularly on non-cercopithecine species which are heavily underrepresented in this review, is therefore needed to determine 1) the occurrence of BSBs in relation to male monopolisation potential, 2) the occurrence of BSBs in relation to female spatial cohesion, 3) whether BSBs are found in multi-layered societies, and whether this depends on secondary female dispersal, 4) whether the balance in male or female investment in BSBs depends on female reproductive status; 5) determinants of continuing / stopping BSBs after a lactation period; and 6) the influence of (secondary) female dispersal on between-sex behaviour and eventual BSBs. These data are needed to test the validity of the proposed link of between-sex leverage and BSBs. In addition, applying this framework to non-primate species living in permanent social groups will inform about its generalizability and will form an evolutionary independent test of this idea.

## CRedit authorship contribution statement

**Elisabeth H.M. Sterck:** Writing – original draft, Visualization, Methodology, Investigation, Conceptualization. **Catherine Crockford:** Writing – review & editing, Conceptualization. **Julia Fischer:** Writing – review & editing, Conceptualization. **Jorg J.M. Massen:** Writing – review & editing, Conceptualization. **Barbara Tiddi:** Writing – review & editing, Conceptualization. **Susan Perry:** Writing – review & editing, Conceptualization. **Cédric Sueur:** Writing – review & editing, Conceptualization. **Oliver Schülke:** Writing – review & editing, Funding acquisition, Conceptualization. **Julia Ostner:** Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Conceptualization.

## Declaration of competing interest

None.

## Acknowledgements

This manuscript was conceived during a Think Tank on “Primate Social Relationships” funded by the Leibniz ScienceCampus “Primate Cognition” and benefitted from the DFG (SFB 1528 - Cognition of Interaction - Project-ID 454648639). We thank Elizabeth Archie, Filippo Aureli, Thore Bergman, Lauren Brent, James Higham, Liza Moscovice, and Gabriele Schino for sharing their ideas with us, Francisca van Hassel for help with the figures, and the editor and two reviewers for insightful comments on the manuscript.

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