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Social and reproductive conflicts between the sexes in mandrills

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*A deep, thoughtful quote
full of meaning*

Middle-aged male
intelligentsia member

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Abstract

The social and sexual conflicts between the sexes can shape the social and reproductive systems of animals. Physical asymmetries often allow males to socially dominate females and use sexually coercive strategies to impose their choice. However, females may resist male strategies through behavioural adaptations and with the aid of their social partners. Such male and female behaviours are widespread across different taxa but their investigation demands systematic data collection over long periods of time. The present thesis examines the nature of social and sexual relationships between females and males in mandrills (*Mandrillus sphinx*), using a 9-year dataset. Mandrills live in large polygynandrous groups and exhibit extreme male biased sexual size dimorphism. Yet, philopatric females maintain strong social bonds and occasionally form coalitions against males. Therefore, the study of social and sexual conflicts between the sexes and the influence of the social environment on these conflicts appears highly relevant in this species. Given the fragmentary understanding of the evolutionary processes promoting dominance skew in favour of one sex, the first chapter investigates the dominance dynamics between the sexes (*Chapter 1*). Female mandrills were found to outrank on average 11% of males, adding to a handful of recent studies which draw a dynamic landscape where several factors may influence intersexual dominance, while the intersexual hierarchy represented an interdigitation of the male and female intrasexual hierarchies. Additionally, social integration in the female social network was found to promote the dominance status of both males and females. The other two chapters investigate the expression and nature of sexual coercion (*Chapter 2*) and the effect of a female's social bonds on the coercion she receives from males (*Chapter 3*). The results suggested that male mandrills use intimidation, a form of sexual coercion that improves male mating success in the long term. Sexual intimidation has been previously reported in only two other (primate) species, and these results indicate that it may appear more often than previously envisaged in sexually dimorphic mammals that live in multimale-multifemale groups. Moreover, higher-ranking and more socially bonded females (with males or other females) received more male coercion, mostly by their male partners and high-ranking males. Hence, male and female mandrills may vary in their propensities to use or receive coercion, respectively, and females seem to experience trade-offs between their social bonds and the male sexual coercion they receive. Altogether, intersexual relationships seem to represent an arms race between the sexes for social and reproductive control which likely reinforce the same evolutionary feedback loop.

General introduction

Life in social groups, except the well-documented benefits such as mutual aid (Kropotkin, 1902), sets the stage for competition for essential resources among a group's members (West-Eberhard, 1979). Social competition may occur in a variety of contexts, over reproduction (e.g. mates or parental care) or survival (e.g. food or space; West-Eberhard, 1979; West-Eberhard, 1983; Stockley and Bro-Jørgensen, 2011; Clutton-Brock and Huchard, 2013b) and its intensity can vary substantially across different species. In despotic societies resources may be unequally distributed among competitors (e.g. reproduction in male mandrills (*Mandrillus sphinx*): Charpentier et al., 2020; food in female olive baboons (*Papio anubis*): Barton and Whiten, 1993), while in more egalitarian societies individuals may share resources equally (e.g. reproduction in African lionesses (*Panthera leo*): Packer, Pusey, and Eberly, 2001; or female banded mongooses (*Mungos mungo*): de Luca and Ginsberg, 2001). Such competition may take different forms ranging from *contests* where the prevailing competitor gets the bulk of the resource at stake and the defeated competitor is deprived of it, to *scramble* where competitors share equal amounts of a finite resource which runs out faster when the number of competitors increases (Nicholson, 1954). Hence, demographic parameters, particularly population density and sex-ratio, may influence the intensity of competition within a population (Jirotkul, 1999; Lukas and Clutton-Brock, 2014). Finally, the different forms of competition can, in turn, impact the evolution of different social and reproductive systems (monogamous, polygamous, polygynandrous etc; Lyon and Montgomerie, 2012; Clutton-Brock and Huchard, 2013b). Competition particularly over reproduction (either between or within the sexes) which determines the way that reproductive opportunities are distributed among a group's members (Reeve, Emlen, and Keller, 1998) may shape the social landscape of a species; for example the use of sexually coercive strategies by males which aim to increase their

reproductive success may promote the evolution of polygyny in mammals (Cassini, 2020).

Power

The outcomes of social competition reflect asymmetries in power, that is, in the ability to elicit certain behaviours from others (Box 1). Power can be divided into ‘decisional’ (e.g. leadership) and ‘resource holding’ (e.g. based on strength; Smith and Parker, 1976; Davidian et al., 2022). An individual holds decisional power when it can influence collective behaviours such as group movement, foraging or inter-group conflict (Smith et al., 2021; Tibbetts, Pardo-Sanchez, and Weise, 2022). Conversely, an individual

Box 1: Power

Power is a concept long used in political science describing asymmetric dyadic relationships (Simon, 1953) but it has only recently introduced in the studies of animal behaviour. It is defined as “*a phenomenon arising from an asymmetry in a dyad that allows one individual to make another do something*” (Lewis, 2018) and constitutes an inclusive concept comprising both dominance (Box 2) and leverage (Box 3; Lewis, 2002).

holds resource-holding power when it can use coercion (Hand, 1986; Lewis, 2002; Beekman, Komdeur, and Ratnieks, 2003), deception, i.e. manipulation of the information available to others (Bro-Jørgensen, 2011) or trade, i.e. bargain of resources that can not be taken by force (Hand, 1986; Lewis, 2002), to control certain resources over its competitors (Davidian et al., 2022). Although the outcomes of inter-individual competition can be influenced by both types of power, the role of resource-holding power in individual survival and reproduction is likely more decisive than the role of decisional power (Smith et al., 2016; Cheng and Tracy, 2020).

Power is commonly studied in each sex separately due to the distinct processes establishing power relationships within sex in certain species. In females, power is often inherited or based on social support while in males it is fight-based (Clutton-Brock and Huchard, 2013b; Tibbetts, Pardo-Sanchez, and Weise, 2022). Moreover, studies of power relationships have traditionally focused on different drivers in each sex: ecological such as food distribution for females (Sterck, Watts, and van Schaik, 1997; see also: Stockley

and Bro-Jørgensen, 2011) but mating related and relevant to reproductive skew for males (Cowlshaw and Dunbar, 1991). Social groups, however, are often composed of individuals of both sexes and thus, females and males may compete over the same resources. Recent studies highlight the existence of a continuum of male-female power relationships (Surbeck and Hohmann, 2013; Young et al., 2017; Hemelrijk et al., 2020) suggesting that intersexual competition is widespread and all the members of one sex do not always overpower all the members of the other sex as it is often assumed due to sexual (size) dimorphism (Lewis, 2020). Therefore, studies of intersexual power may prove to be highly useful in the elucidation of the social and reproductive struggles between females and males, and can offer insightful information on sex differences in social competition across species.

Box 2: Dominance

Previous studies have used different definitions of dominance (Drews, 1993). This work adopts the predominant one that describes dominance as power based upon force or the threat of force (Lewis, 2002; Lewis, 2018).

Dominance can be distinguished in *intrinsic*, when it is based on an individual's own traits and potential to use force (e.g. size, age or fighting experience), and *derived* when it is not based on such intrinsic attributes of the individual but, for example, on coalitions or used tools (Hand, 1986).

High or low dominance rank of an individual refers to its position in a hierarchy and it is a relative measure that depends on group composition, rather than an absolute individual property (Drews, 1993).

When the physical attributes such as body size and strength determine inter-individual power relationships, resource-holding power is often reflected in the outcomes of contest competition which takes the form of agonistic - aggressive or submissive - interactions. Such interactions, although more evident in male-male competition, can appear with similar intensity and frequency in female-female competition (Stockley and Bro-Jørgensen, 2011) while the nature and frequency of agonistic interactions between the sexes are less documented. When an individual appears to consistently 'win' such interactions against another individual, then the first one is considered dominant (Box 2) over the latter. Recent studies in different species that have constructed social hierarchies to

examine intersexual power differentials have revealed that intersexual dominance can either be skewed in favour of males or females, or it can be more balanced between the sexes (Kalbitzer et al., 2015; Norscia and Palagi, 2015; Young et al., 2017; Hemelrijk et al., 2020; Izar et al., 2021). When one sex is not strictly dominant over the other, intersexual dominance dynamics may vary across different contexts within species (birds: Smith, 1982; Jawor, 2000; primates: Dunham, 2008; Hemelrijk, Wantia, and Isler, 2008; Ferrari, 2009; other mammals: Murie and Harris, 1988; Koren, Mokady, and Geffen, 2006; Hewitt, Macdonald, and Dugdale, 2009a).

Resource-holding power may also describe a relationship where an individual controls a valuable resource that can not be taken by force and trades it with another individuals (Lewis, 2002). Examples of such resources include information, skills, genes or services like grooming (Hand, 1986; Lewis, 2002). In intersexual relationships, this mechanism of trade often refers to the leverage¹ (Box 3) that females can have over males

Box 3: Leverage

Power that can arise from asymmetries in the control of inalienable resources between trading individuals (Lewis, 2002).

while the valuable resource that can not be taken by force is typically related to reproduction (e.g fertilizable eggs; Lewis, 2002; Lewis, 2018; Lewis, 2020). In the context of these ‘mating markets’ (Noë and Hammerstein, 1994; Gumert, 2007) males may be less aggressive and more compliant in order to gain access to females which may hold more power during periods of fertility (Davidian et al., 2022). Lastly, recent studies suggest that females may have more leverage in species with pronounced female power and low sexual size dimorphism (Surbeck and Hohmann, 2013; Lewis, 2020), although the causal relationships of these phenomena is not fully understood.

Sexual selection

Although social competition does not only occur over reproduction (West-Eberhard, 1979; Chapman et al., 2003), in the theory of evolution and natural selection, reproduction constitutes a determining resource for the fitness of an individual (Darwin, 1859). Thus,

¹

relevant studies often focus on competition over reproduction investigating usually two distinct - but related - concepts: reproductive competition and reproductive control. Reproductive competition - competition over resources essential for reproduction (Clutton-Brock, 2007) - is widespread in sexually reproducing species and usually occurs between individuals of the same sex for access, for example, to mates (Lyon and Montgomerie, 2012; West-Eberhard, 1979). Conversely, individuals of the opposite sex may compete to obtain higher reproductive control, which offers to more powerful individuals control over when and with whom to mate (Box 4; Beekman, Komdeur, and Ratnieks, 2003).

Box 4: Reproductive control

The extent of control that an individual has over (i) its own reproduction and determines the occurrence, timing and frequency of mating and/or (ii) the reproduction of others and determines, for example, the number and identity of mates (Beekman, Komdeur, and Ratnieks, 2003; Davidian et al., 2022).

Reproductive competition and reproductive control lie at the core of the theory of sexual selection (Box 5), a form of selection describing the processes where members of one sex compete among them for access to reproduction (intrasexual competition) and choose their mates of the

other sex (mate choice; Darwin, 1871). In most mammals, females invest a higher amount of time and energy in each reproduction event (gestation and parental care) than males (Trivers, 1972; Gittleman and Thompson, 1988) and hence, they often constitute the limiting sex, especially when the ratio of fertile females to males favours the latter ones (Darwin, 1871). Consequently, male intrasexual competition for access to females is often evident. Intense male intrasexual competition often leads to the evolution of secondary sexual characters, typically armaments (e.g. canines or horns) and ornaments, that are advantageous for males to the competition with other males while they may also be chosen by females as indicators of male quality (Darwin, 1871). Female intrasexual competition, at the other end of the spectrum, is often characterized by seldom escalated contests and female secondary sexual characters are less extreme (Clutton-Brock and Huchard, 2013a) rendering intrasexual selection in females presumably harder to study (Kappeler and Schaik, 2004). Nevertheless, the inter-individual variation in reproductive success and the intensity of intrasexual competition in females can be as high as in males (Clutton-Brock, 2009) because individuals from either sex strive to increase their

fitness under selection pressures that operate on both sexes similarly (Clutton-Brock and Huchard, 2013b).

High-ranking males often monopolise reproductive opportunities and traditional models of sexual selection in mammals have granted much control to these males (Clutton-Brock, 1998; Clutton-Brock, 2007; Clutton-Brock and Huchard, 2013a). According to the priority of access model, the alpha (highest-ranking) male monopolises oestrous females in priority, while the next higher-ranking males will enjoy mating opportunities only if several females

Box 5: Sexual selection

Sexual selection is a form of selection which does not depend on “*a struggle for existence in relation to other organic beings or to external conditions*” (Darwin, 1859) but rather on “*the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction.*” (Darwin, 1871)

are synchronously receptive (Altmann, 1962). Alternatively, the concession models assume that the alpha male is in full control of all reproductions but concedes some of them to subordinate males, in exchange of their cooperation to defend the group against extra-group males (Snyder-Mackler, Alberts, and Bergman, 2012). These models work under the implicit assumption that female strategies have only a negligible influence on mating patterns. However, a combination of physiological and behavioural adaptations allow females to express mate choice and influence the outcomes of reproduction (Paul, 2002; Drea and Wallen, 2003). For example, females can solicit mating from different males (Dixson, 1998; Hrdy, 1979) or they can incite male-male competition that may allow them to mate only with superior males (Cox and Le Boeuf, 1977). Moreover, females may have a greater control on post-copulation processes such as sperm competition (Parker, 1970) which might be harder to identify compared to pre-copulation processes of sexual selection like sexual solicitations (Eberhard, 2009). Altogether, the mechanisms which allow both male and female reproductive strategies to co-occur, given that they may operate in opposing directions, constitute an evolutionary puzzle only partially understood.

Sexual conflict

Extensive evidence highlight that intersexual interactions are characterized by conflict of interests due to commonly divergent evolutionary - reproductive or genetic - interests of males and females (Trivers, 1972; Parker, 1979; Smuts and Smuts, 1993; Chapman et al., 2003). In particular, the reproductive success of females and males is often limited by distinct factors. Females face higher reproduction costs, for example due to gestation in mammals while males are often limited only by the number of mating partners (Bateman, 1948). This asymmetry can lead to sexually antagonistic coevolution (Clutton-Brock and Parker, 1995b), an arms race between the sexes which may prevent evolutionary equilibrium. This phenomenon, termed sexual conflict (Box 6), may shape the mating and reproductive strategies in mammalian societies (Parker, 1979; Muller, Kahlenberg, and Wrangham, 2009) and it can influence a species' behaviour, anatomy and life-history (Bonduriansky et al., 2008) that, in turn, can lead to sexual dimorphism or even speciation (Parker and Partridge, 1998; Panhuis et al., 2001). Sexual conflict can function either over a specific locus, when females and males have different optima for a trait, or between sex-specific loci which determine female or male traits (Parker and Partridge, 1998). Hence, sexual conflict can determine traits advantageous for males but adverse for females and vice versa (Parker and Partridge, 1998). The imprint of previous conflict on such traits makes the disambiguation of sexual conflict anything but trivial.

Box 6: Sexual conflict

Sexual conflict describes the conflict of evolutionary interests between the sexes (Parker, 1979).

Sexual conflict is often expressed during mating. In order to improve their fitness, males produce many small gametes and aim to increase their mating and reproductive rates (Trivers, 1972) while females are more selective, targeting mates of higher quality and they produce few large gametes (Lessells, 2006). In this context, males might coerce females to mate with them (Box 7; Smuts and Smuts, 1993; Clutton-Brock and Parker, 1995b; Stumpf et al., 2011). The effect of sexual coercion can be direct, when it increases the mating success of the coercer with the female victim, or indirect when it decreases the mating probability of the victim with other males (Smuts and Smuts, 1993). In addition, the benefits for the male coercer can be immediate or delayed. In species that do not form long-lasting intersexual relationships males may have imme-

diate benefits by using coercive strategies that lead to mating directly after aggression (forced copulation or sexual harassment; Box 8), while in species that form long-lasting intersexual relationships males may assault females targeting to future mating activity with them (sexual intimidation or punishment; Box 8; Clutton-Brock and Parker, 1995b).

Sexual coercion has been previously described as a third form of sexual selection - along with intrasexual competition and mate choice (Smuts and Smuts, 1993) - because of its impact on the reproductive outcomes and the mating system of different species. Male coercion may restrict female mate choice and impose further significant costs to females like higher stress levels of injuries (Smuts and Smuts, 1993; Clutton-Brock and Parker, 1995b). Females may attempt to reduce male coercion and its costs through certain anatomical or behavioural adaptations. For example, female (genitalia) morphology may prevent mating without cooperation of the female (Drea and Wallen, 2003) or females may retaliate against males, potentially with the aid of conspecifics (Fox, 2002). In addition, females may profit and increase their fitness by producing more coercive male offspring who have higher reproductive success ('sexy son hypothesis': Fisher, 1915). Finally, in order to reduce male assaults, females may mate preferentially with males who direct most coercion at them. Hence, soliciting various males or picking particular ones may not only reflect the expression of female mate choice, but also the outcome of sexual coercion (Muller et al., 2011).

Box 7: Sexual coercion

The “*use by a male of force, or threat of force, that functions to increase the chances that a female will mate with him at a time when she is likely to be fertile, and to decrease the chances that she will mate with other males, at some cost to the female.*” (Smuts and Smuts, 1993)

Social bonds

In social animals, both power and reproductive control can be influenced by social strategies and the social support that individuals enjoy within their social group (Kappeler, 1993; Cassini, 2020). Such social support is often indexed by affiliative bonds: individuals who share a bond are likely to offer social support to each other during conflicts

Box 8: The main forms of sexual coercion

Short-term strategies

Forced copulation: A male physically restrains a female and copulates with her by force, taking advantage of his physical superiority.

Sexual harassment: A male (repeatedly) assaults a female which complies and copulates immediately.

Long-term strategies

Sexual intimidation: A male assaults a female (over long periods) in order to increase the probability that she will mate with him in the future (when she will be fertile).

Sexual punishment: A male assaults a female that copulated with another male in order to decrease the probability that she will copulate again with other males than him.

Infanticide: A male kills the dependent (non-weaned) infant of a female in order to increase the probability that she will resume cycling shortly after.

(Smuts and Smuts, 1993; Clutton-Brock and Parker, 1995b)

and events of social competition (Vullioud et al., 2019; Parish, De Waal, and Haig, 2000). Within social groups, social bonds can be highly differentiated with individuals interacting preferentially with a fraction of their groupmates but never with others. In female philopatric species, for example, females often form the strongest bonds with close kin and/or with females of similar dominance rank to themselves, like in geladas (*Theropithecus gelada*; le Roux, Beehner, and Bergman, 2011; Tinsley Johnson et al., 2014) or yellow baboons (*Papio cynocephalus*; Silk, Alberts, and Altmann, 2006). These bonds may benefit the connected individuals directly by increasing their own fitness or indirectly by increasing the fitness of their partners (see: Hamilton, 1963). Recent studies suggest that more bonded individuals can enjoy long-term fitness benefits including, for example, enhanced reproductive success in wire-tailed manakins (*Pipra filicauda*; Ryder et al., 2009) and Assamese macaques (*Macaca assamensis*; Schülke et al., 2010), infant survival in yellow baboons (Silk, Alberts, and Altmann, 2003) or further privileges such as access

to resources in killer whales (*Orcinus orca*; Ellis et al., 2017).

Social bonds may also be associated with dominance rank which, in turn, is associated to several fitness benefits (Majolo et al., 2012). The formation of dominance hierarchies in animal groups depends on individual attributes but also on social attributes and interactions (Box 2; Chase et al., 2002). In social species, such interactions may involve more than one individual in each competing side and their outcomes can be highly influenced by the social support the involved individuals enjoy from members of either sex (Clutton-Brock and Huchard, 2013b). For example, in greylag geese (*Anser anser*) and in other species of gees, the social support that an individual enjoys from kin or pair partners has a strong impact on its dominance status (Weiß and Kotrschal, 2004). Particularly in species characterized by pronounced levels of female dominance over males, social support may have an increased impact on dominance dynamics. Notably, spotted hyenas (*Crocuta crocuta*) who enjoy greater social support dominate more one-on-one interactions across different contexts (Vullioud et al., 2019), while female bonobos often form coalition and dominate males (Parish, De Waal, and Haig, 2000).

Finally, a few previous studies suggest that social bonds may also protect females from sexual coercion. Since the first formal documentation of sexual coercion, the association of females with particular males was described as the most common strategy that female mammals may use to reduce their vulnerability in coercive male mating strategies (Smuts and Smuts, 1993). For example, in yellow baboons (Palombit, 1999; Nguyen et al., 2009) and other primates (Van Schaik and Kappeler, 1997), females form close affiliative bonds with particular males that protect these females and their infants from potential attacks from other males. Similarly, in orangutans, females who maintain close associations with males receive significantly lower rates of male sexual coercion (Fox, 2002). As a consequence, females may prefer to associate or mate with males who can protect their infants and themselves from the aggression of other males more efficiently (Smuts and Smuts, 1993). In addition, female-female bonds could potentially also protect females from male sexual coercion (Smuts and Smuts, 1993). In feral horses, more socially integrated females receive less male harassment (Cameron, Setsaas, and Linklater, 2009) but it remains unclear if this occurs in a sexual context.

Studying monkeys

Once habituated to human observers, primate groups can be monitored and studied easier than other animal groups (e.g. of birds, fishes or elusive and nocturnal mammals) and long-term research projects can use fine-grained ethograms in order to study the complexity of their social and sexual behaviours. Their slow life-histories and low reproductive rates including increased investment in each event of reproduction (Wright, 1990), allow the study of long-term strategies that shape social and sexual relationships. Finally, comparative studies may profit from the diversity of their social and mating systems (solitary, pair living, group living) and the variety in group sizes, sex ratios or dispersal patterns (male, female or bisexual; Kappeler and van Schaik, 2002) to elucidate the conditions that favour the evolution of different patterns in intersexual relationships within different social landscapes.

In social long-living species, like non-human primates, agonistic interactions can offer future benefits to the winner of a conflict (Clutton-Brock and Parker, 1995a) and observations of such repeated - over long periods of time - interactions for access to resources allow the construction of dominance hierarchies. Hence, dyadic relationships which can be highly differentiated reflecting the complex socio-cognitive skills of primates (Cheney, Seyfarth, and Smuts, 1986; Barrett, Henzi, and Dunbar, 2003), can be analysed in the light of interaction history and dominance differentials. Particularly intersexual dominance in primates shows a great variety and often is at odds with the traditional consideration of male dominance. For example, in species like capuchin (Izar et al., 2021) or vervet monkeys (*Chlorocebus pygerythrus*; Hemelrijk et al., 2020) females can occasionally dominate males, while in other species, including the majority of lemurs, female dominance over males is the norm (Dunham, 2008; Lewis, 2020). Finally, female primates can also have leverage related power over males (Lewis, 2018).

Offspring production and care are particularly time and energetically costly for female primates due to (i) long periods of gestation and lactation (Gittleman and Thompson, 1988) and (ii) the importance of parental investment (Wright, 1990). Paternal care is also more common in primates than in other mammalian orders (Kleiman and Malcolm, 1981), taking different forms such as protection against infanticide (Van Schaik and Janson,

2000) or support of offspring during conflicts (Kulik et al., 2012). Therefore, females may strive to express mate choice in order to secure the necessary resources (e.g. high quality partners) for their reproduction, giving rise to sexual conflict with males who attempt to increase their overall reproductive rate, often via promiscuity.

Sexual conflict shows a great variety even among closely related primate species. Within the genus *Papio*, there are species characterized by different forms of sexual coercion and severe aggression towards females (e.g. hamadryas (*Papio hamadryas hamadryas*): Swedell and Schreier, 2009; and chacma baboons (*Papio ursinus*): Baniel, Cowlshaw, and Huchard, 2017) and species characterized by considerably lower rates of male aggression towards females (e.g. Guinea baboons (*Papio papio*): Goffe, Zinner, and Fischer, 2016). Male chimpanzees, similarly to men², are sexually coercive, and males in general dominate females, in contrast to bonobos, the other species of the genus *Pan*, where females dominate most males and sexual coercion is absent (Muller and Wrangham, 2009). This diversity renders primates a suitable order to study the factors which promote the expression of sexual coercion.

Nonetheless, the majority of empirical evidence of sexual conflict and sexual coercion to date comes either from studies on invertebrates or, less often, on non-mammalian vertebrates which use short-term mating strategies (Box 8; Aloise King, Banks, and Brooks, 2013). Much less is known on species with slow life-histories, like non-human primates, which may use long-term strategies (Muller and Wrangham, 2009) given the long-lasting social relationships that they form. The difficulty to habituate primates in the wild and the consistently recorded behavioural data needed for studies on sexual conflict, may account for this deficiency. In addition, although a handful of previous studies on sexual coercion in primates have focused on the variation of coercive strategies (Reddy et al., 2021) and their reproductive benefits for males (e.g. increased reproductive success in

²The reproduction of women is often controlled by men: intimate partner violence and sexual aggression are common in human societies (Basile, 2002; Muller and Wrangham, 2009) while the levels of male sexual aggression a woman experiences depend on different factors including her social bonds (Smuts, 1992). Therefore, investigating the evolutionary paths and mechanisms of social constraints on sexual behaviour and their adaptive significance in non-human primates, may shed some light on the evolutionary roots of human sexual aggression. Notably, human behaviour is characterized by remarkable flexibility and can be shaped by the interaction of genes, environment and culture. The study of the potential adaptive value of sexual aggression by no means renders its exertion ethically justified. Conversely, such studies may assist in the understanding of the conditions (where, when and how) that promote - and potentially in coordinated actions that can reduce - the expression of human sexual aggression.

chimpanzees; Feldblum et al., 2014) much less is known about the female perspective. First, females potentially receive different levels of male sexual coercion depending on their physical, behavioural or social attributes. Second, the reproductive trade-offs and the fitness consequences (e.g. lower reproductive success) that female primates experience due to sexual coercion remain widely unknown.

The intensity of sexual coercion can vary among or even within primate populations (Pieta, 2008; Kaburu and Newton-Fisher, 2015; Watts, 2022) and male aggression rates may depend, for example, on cultural traits of a group (Sapolsky and Share, 2004). When the studies of sexual coercion on chimpanzees were first published (Muller et al., 2007; Muller et al., 2011), supposedly cast doubt on previous evidence on chimpanzee female choice (Stumpf and Boesch, 2006). Since then, however, female choice in chimpanzees has been documented anew, showing an inter-population variation in mating strategies (Pieta, 2008; Kaburu and Newton-Fisher, 2015; Watts, 2022). It seems, consequently, that male sexually coercive strategies do not necessarily rule out the expression of female mate choice but both phenomena may co-occur. This highlights the caution needed in studies of sexual selection when disentangling the conflicts between the sexes.

Study aims

The central focus of this thesis is the social and reproductive conflicts between wild females and males of a social primate, the mandrill (*Mandrillus sphinx*). The first chapter investigates the dominance hierarchy of a mandrill group taking into account agonistic interactions among the adult group members of both sexes. The first goal of this chapter is to clarify if females can outrank males despite the extreme male biased sexual size dimorphism of mandrills (see *Study species* section below). Then, it aims to describe the hierarchical structure of the group and clarify if the rules that govern the formation of intrasexual hierarchies are the same that govern the formation of intersexual hierarchy, by testing if the position of an individual of either sex in the intrasexual hierarchy reflects its position in the intersexual one. Finally, this chapter sheds light on certain factors - including both male and female individual attributes - that can influence the dominance relationships (who outranks who) or the outcome of conflicts between the members of

a certain heterosexual dyad. In particular, the effect of the social bonds of females and males is investigated, predicting that such bonds can impact intersexual dominance dynamics and philopatric females may depend on them in order to confront males who are likely less socially integrated. Second, it tests if the seasonal changes (mating vs birth season; or the group sex ratio) which may reflect both motivational shifts or changes in group demography can influence the dominance dynamics in mandrills, as suggested from studies on other primates (Hemelrijk et al., 2020; Izar et al., 2021). Last but not least, in order to test if female mandrills hold some leverage related power over males, it tests if females are more dominant over males when they are sexually receptive.

In certain baboon species which are closely related to mandrills, males use different sexually coercive strategies to increase their mating success (Swedell and Schreier, 2009; Baniel, Cowlshaw, and Huchard, 2017). In addition, the sexual size dimorphism of mandrills may facilitate the expression of sexual coercion from males. The second chapter of this thesis examines, therefore, if male mandrills use sexual coercion against females to gain mating opportunities, by testing the three predictions of the sexual coercion hypothesis, namely if male aggression (i) particularly targets sexually receptive females, (ii) inflicts costs to these females, and (iii) increases male mating success with the victim. On the one hand, mandrills form multimale-multifemale groups which may allow the expression of long term coercive strategies (Box 8) but on the other hand, many males immigrate seasonally and hence, they may not form long-lasting relationships with females and may adopt short-term coercive strategies against them. The severity of male aggression against females, however, seems low in mandrills. Males have never been observed to force copulation with females while infanticide has not been formally documented (Dezeure, Charpentier, and Huchard, 2022). Based on these observations, this chapter investigates if male mandrills use sexual harassment, intimidation or punishment against females. In contrast to previous studies that used only severe aggression (Muller et al., 2007; Baniel, Cowlshaw, and Huchard, 2017), the potential coercive nature of non-physical threats is also examined, predicting that the extreme physical superiority of male mandrills can render their threats intimidating enough in order to function as sexual coercion against females. Finally, the effect of dominance rank of both male coercers and female victims is investigated, in order to clarify if the propensity to coerce (for males) or to be coerced (for females) is not equal among all individuals as suggested

in other species (Kunz et al., 2021b) and given the high reproductive skew in favour of the highest-ranking male mandrills.

The third chapter follows up on the expression of sexual coercion and focuses on the effect of social and matrilineal bonds of females. Based on evidence from other species suggesting that social bonds can be protective (Smuts and Smuts, 1993; Palombit, 1999; Fox, 2002), the hypothesis that the bonds of female mandrills with males or other females is tested ('protective bonds hypothesis') versus the hypothesis that opposite selective pressures render such bonds costly for females ('costly bonds hypothesis'). In particular, the following predictions are tested: First, females with stronger affiliative bonds with particular males receive less coercion from them because these males can mate with their female partners without coercing them. Second, females which form stronger bonds with all males or their top male partner, receive less coercion from their top coercer or all males respectively because males protect females from coercion from other males. Third, more bonded females with their female groupmates receive less sexual coercion from males because females support more their kin or their partners with whom they share stronger bonds against male coercion.

High-ranking and more bonded female mandrills may have higher reproductive success (Setchell and Jean Wickings, 2006; Charpentier et al., 2012) and males may prefer to mate with females of higher rank and quality (Setchell and Jean Wickings, 2006). Based on this evidence and the result that more integrated females in the female social network receive more male coercion generated by the 'costly bonds hypothesis', in a last step, two indirect and one direct pathway are tested to clarify the relationship of sexual coercion and female social bonds. These pathways correspond to the following predictions: Females receive more male coercion because (a) they are more attractive to males because of their higher reproductive success ('attractiveness hypothesis'), (b) they are more powerful and they have higher retaliation potential ('retaliation hypothesis') and thus males need to assault them more in order to make them comply sexually and (c) they are simply more exposed to coercion because they occupy central positions in the group and interact more with their groupmates - including coercive males - than peripheral females ('public exposure hypothesis').

Study species

Mandrills (Figure 1 & 2) are omnivorous and semi-arboreal primates from the *Cercopithecidae* family that live in equatorial forests of Africa (Abernethy, White, and Wickings, 2002). They are elusive and, as most primates living in forested areas, hard to habituate to the presence of observers. In contrast to traditional approaches that generally studied mandrills in captivity, the present work focuses on the only long-term studied population of wild mandrills (see section *Study population*). It is likely that the intersexual relationships (mating system and social structure) in wild mandrills differ significantly from patterns studied in captivity (Charpentier et al., 2005). First, the provisioning in captivity may loosen certain selective pressures relevant to survival that might impact inter-individual competition among group members. Second, mandrills breed seasonally (Figure 3) and new males enter the social group at the onset of the mating season and most of them leave once the mating season is over (Brockmeyer et al., 2015), a phenomenon absent in captivity.



Figure 1: Baby mandrill



Figure 2: An adult female grooms an adult male mandrill. The sexual size dimorphism and the female sexual swelling are visible.

In contrast to males, female mandrills are philopatric and constitute the core of their large (counting hundreds of individuals: Abernethy, White, and Wickings, 2002) polygynandrous groups (Brockmeyer et al., 2015). Females form strong social bonds with some of their groupmates showing strong biases in favour of close maternal and paternal kin (Charpentier et al., 2020) and these bonds are positively associated to reproductive success (Charpentier et al., 2012). At the other end of the spectrum, the temporal residency of male mandrills in the social group suggests that they are likely less socially integrated than females. Nevertheless, the mating season lasts more than 4 months (broadly from April to September; Dezeure, Charpentier, and Huchard, 2022) meaning that female-male associations relevant to mating can last for long periods and competition over reproduction may last for several months.

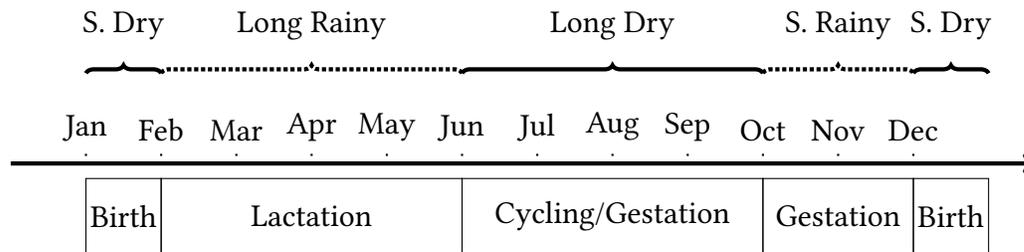


Figure 3: Schematic representation of the general patterns of environmental and reproductive seasonality of the study population (for more details see: Dezeure, Charpentier, and Huchard, 2022). S. Dry: short dry season; S. Rainy: short rainy season.



Figure 4: Male mandrill

Male mandrills compete intensely during the mating season and reproductions are highly skewed in favour the alpha male that monopolises 60-70% of them (Charpentier et al., 2005; Charpentier et al., 2020). High-ranking males mate-guard receptive females which exhibit perineal sexual swellings around ovulation (Figure 2; Setchell, Charpentier, and Wickings, 2005a). Hence, the mating outcomes seem largely controlled by males (Charpentier et al., 2005), while their extreme sexual size dimorphism, with males ~ 3.4 times heavier than females (Figure 2; Setchell et al., 2001), highlights a major physical power asymmetry between the sexes which might facilitate the expression of sexual coercion. Yet, males exhibit extreme secondary sexual characters, including extravagant facial

and hindquarter colouration (Figure 4; Setchell and Jean Wickings, 2005), which suggest that they may have been the target of female mate choice (Setchell, 2016; Setchell, 2005). In addition, observations of female retaliation against male aggression and female coalitions against adult males (Setchell, Knapp, and Wickings, 2006) may underline a considerable effect of social support on the social dynamics among the sexes. Overall, the large polygynandrous groups along with the extreme male-biased sexual size dimorphism and the differentiated female-female bonds and coalitions against males, render the study of intersexual dominance and sexual coercion in mandrills highly relevant.

Study population

In 2002 and 2006, 36 and 29 captive individuals respectively, housed in CIRMF (Centre International de Recherches Médicales de Franceville, Gabon), were released in a park located in Southern Gabon (Lékédi park). In 2003, wild males were already observed to join the group and reproduce with the released females (Peignot et al., 2008) who were observed cycling shortly after their release. In January 2012, the *Mandrillus project* was set up to study the behaviour and ecology of a population of mandrills including some of these individuals, benefiting from their initial habituation to human presence. Shortly after, in June 2012, the group was counting ~120 individuals and in early 2022, only 6 adult females among over 220 individually-recognized individuals were captive-born. Finally, the group's range extended over the years far beyond the park's boundaries in a mosaic area of evergreen forests grasslands and savannahs (Brockmeyer et al., 2015).



Figure 5:
Psychedelic
female mandrill

Seasonal changes in the surrounding area form a distinct pattern of four ecological seasons (Figure 3): a long rainy from February to May, a long-dry from June to September, a short rainy from October to November and a short dry season from December to January.

Data collection

Trained observers perform daily behavioural observations (a combination of ad libitum and 5-min focal observations: Altmann, 1974) on all study individuals. Daily census is also performed recording the presence of each individual in the group and birth or death events, allowing to keep track of the group's demography. The observers usually stay with the group from dawn to dusk recording also its location and movement patterns.

During behavioural observations, sexual and affiliative interactions as well as aggressive encounters and submissive responses are recorded, allowing the construction of dominance hierarchies. Additional information on body condition (e.g. injuries) and details on the reproductive states (sexual swelling, gestation, lactation) of females older than 3 years is also recorded.

In the context of the present work, the ethogram based on which observers perform behavioural observations was enriched. Since 2021, observers record (i) intersexual approach-leave interactions including information on the identities of the individuals responsible for maintaining the proximity, (ii) female interruptions of copulation, as well (iii) 'sex audiences', i.e. the individuals surrounding a copulating dyad. The enriched dataset along with the already long-term data on coalitions, aggression, copulation and affiliation between adult mandrills, may assist answering follow up questions of this work, regarding the latitude of female mandrills to exert mate choice.

For more details on the collection protocol of the data used for each study, see the section of *Methods* of the relevant chapter.

Chapter 1

Dynamics of intersexual dominance in a highly dimorphic primate

Authors

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Abstract

In sexually dimorphic mammals, intersexual dominance measured by the probability that members of one sex gain conflicts over members of the other sex, is often skewed in favor of males due to their physical superiority over females. However, even in male-dominated species, several factors may influence intersexual dominance. Here, we use an 8-year dataset to examine the dynamics of intersexual dominance in wild-living mandrills (*Mandrillus sphinx*). Mandrills exhibit extreme sexual size dimorphism but females show pronounced kin-differentiated social relationships and occasionally form coalitions against males. We established the intersexual dominance hierarchy across consecutive 6-months blocks (representing either mating or birth seasons), and found that on average, an adult female outranks 11% of males. In a second step, we show that the intrasexual rank of an individual predicts its position in the intersexual hierarchy, underlining an interdigitation of the male and female intrasexual hierarchies. Further, we show that social integration, through affiliation with female groupmates, promotes the dominance status of both males and females. Finally, in accordance with studies on other primate species, female mandrills appear to have a higher probability to outrank males (i) during the mating season, when males are more numerous than in the birth season, and (ii) when males are young or old adults, than when they are in their prime. These results extend our understanding of intersexual dominance by showing that female mandrills are occasionally able to outrank some males who are considerably larger than them and can, through their affiliative relationships among them and with males, influence the intersexual dominance hierarchy.

1.1 Introduction

Intersexual hierarchies reflect sexual asymmetries in the outcome of agonistic interactions, which are often biased toward males. Despite their importance for the social structure, mating strategies and life-history of a species (Parker, 2006), studies of dominance hierarchies have long been restricted to intrasexual contexts (Ellis, 1995; Davidian et al., 2022), sometimes considering by default that males were dominant over all fe-

males in the intersexual hierarchy (Lewis, 2018). While intersexual dominance has long been polarized into male- vs female-dominant species, recent studies that have quantified intersexual dominance via the construction of intersexual hierarchies draw a more nuanced and dynamic landscape (Lewis, 2020; Davidian et al., 2022; Kappeler et al., in press), where intersexual dominance varies along a continuum, including more balanced male-female dominance relationships (e.g. Hemelrijk et al., 2020). Except for the handful of well-known cases where female-biased dominance has long been reported (bonobos (*Pan paniscus*): Parish, De Waal, and Haig, 2000; most lemurs: Kappeler, 1993; Petty and Drea, 2015; spotted hyenas (*Crocuta crocuta*): Kruuk, 1972), there is a growing list of species with circumstantial or contextual female dominance over males (primates: Dunham, 2008; Hemelrijk, Wantia, and Isler, 2008; Izar et al., 2021; Ferrari, 2009; small mammals: Murie and Harris, 1988; Koren, Mokady, and Geffen, 2006; Hewitt, Macdonald, and Dugdale, 2009a; birds: Smith, 1982; Jawor, 2000; see also Hand, 1986). Our understanding of why some intersexual dominance is biased towards females in some species, and towards males in others is still fragmentary and often relies on taxon-specific hypotheses (Lewis, 2018; Kappeler and Fichtel, 2015; Davidian et al., 2022).

There are still several sources of uncertainty concerning the structural properties of intersexual dominance hierarchies. First, it has long been unclear whether intrasexual dominance rank predicts intersexual rank because intrasexual agonistic interactions may target different resources and dominance relationships may be established and maintained through different mechanisms depending on the sex (e.g. inherited vs. fight-based hierarchies; Clutton-Brock and Huchard, 2013b; Tibbetts, Pardo-Sanchez, and Weise, 2022). A recent analysis including several mammal species however indicates that intersexual rank may often reflect intrasexual rank (Kappeler et al., in press). Second, dominance hierarchies based on matrices constructed with different methods can lead to different results (Lewis, 2002). Agonistic interactions may have different forms and variable outcomes. Although standardized methods to quantify intersexual dominance have been recently proposed (Kappeler et al., in press), previous studies often mix, for example “undecided” (i.e. not systematically followed by submissive behaviors) and “decided” interactions or even aggressive and submissive behaviors (e.g. Hemelrijk et al., 2020) to construct dominance hierarchies which may affect the comparability of the results. Aggression is often expressed under tensed circumstances during social conflicts while sub-

mission is regularly, and often spontaneously, expressed in ritualized contexts outside situations of social tension, and may constitute more reliable cues of perceived dominance relationships (Kappeler et al., in press). Additionally, in species with dominance biased towards males, females may threaten or direct aggression towards males during conflicts or tensed situations when they are aroused, while they may be unable to elicit male submission in routine situations (French et al., 2013); in contrast, in Verreaux sifakas (*Propithecus verreauxi*) where females are strictly dominant over males, nearly 90% of spontaneous submissions are expressed by males towards females, while females win only about 1/3 of heterosexual conflicts (Lewis, Bueno, and Di Fiore, in press). Overall, females may appear more or less dominant over males in social hierarchies built using different types of social interactions.

Several factors other than aggressiveness or physical characteristics (e.g. size or strength, which are not necessary conditions for female empowerment) have been suggested to be influential in the outcome of intersexual conflicts (Lewis, 2002; Davidian et al., 2022). Specifically, inconsistencies in the outcome of such conflicts occur both between and within dyads (i.e. it's not always the same dyad member who wins the conflict; Hemelrijk et al., 2020; Young et al., 2017; Chase et al., 2002; Hewitt, Macdonald, and Dugdale, 2009b; Lewis, 2022), suggesting that ecological pressures may affect intersexual dominance within species. Females may be more or less dominant depending on their reproductive state: for example, female mouse lemurs win more intersexual conflicts during the reproductive season than outside (Hohenbrink et al., 2016), and in many monogamous birds females are more dominant over males when they are sexually receptive (Smith, 1980). These phenomena likely reflect leverage, a source of power asymmetries between the sexes which emerges from one sex having control over a resource that is valuable for the other sex and cannot be taken by force, such as fertilizable eggs (Lewis, 2002; Lewis, 2018; Lewis, 2020). Leverage may affect intersexual dominance dynamics as males may be more cooperative or compliant in order to gain access to fertile females, in a form of trade described as 'mating market' (Noë and Hammerstein, 1994; Gumert, 2007). This effect may only be confined to periods of sexual receptivity or become more permanent when both sexes live in stable groups as in bonobos (Surbeck and Hohmann, 2013) or vervet monkeys (*Chlorocebus pygerythrus*; Young et al., 2017; Davidian et al., 2022). Nevertheless, in species with low female reproductive control - control over who

to mate with, and when – and specifically where males can coerce matings by threatening or monopolizing females (Muller et al., 2007; Baniel, Cowlshaw, and Huchard, 2017), such leverage may be absent or minimal.

Second, recent studies have shown that the group sex-ratio influences intersexual dominance and that females dominate more males when the number of males in the group increases (Lewis, 2020; Izar et al., 2021; Hemelrijk et al., 2020). In primates, female dominance over males may emerge from the so-called ‘winner and loser effects’ where more males in a group fight more, causing more losses and injuries in subordinate males who may eventually submit to females (Hemelrijk, Wantia, and Isler, 2008; but see also: Bonabeau, 1999). Alternatively, such an effect may reflect the dynamics of mating markets (Noë and Hammerstein, 1994; Gumert, 2007), where fluctuating sex-ratios affect the relative sex-based leverage gained by fertile females, as the relative value of fertilizable eggs increases with their rarity, i.e. when there are less fertile females for a larger number of males.

Finally, social support and coalitions can also influence the outcome of agonistic interactions in different taxa and more socially-integrated individuals are more likely to win a conflict even if their supporters are not immediately involved (Markham et al., 2015; Weiß and Kotrschal, 2004). Social support therefore shapes emerging hierarchies and reinforces established ones (Bissonnette, de Vries, and van Schaik, 2009; Vulllioud et al., 2019; Strauss and Holekamp, 2019). In mammals, female philopatry is frequent (Greenwood, 1980), and typically reflected by females having higher relatedness and social connectedness to their groupmates than immigrant males. As a result, philopatric females often ground their dominance relationships on social support (Clutton-Brock and Huchard, 2013a), which may influence the outcome of intersexual conflicts, as shown in spotted hyenas (Vulllioud et al., 2019). As a result, greater social support may bias the outcome of intersexual conflicts towards females in species characterized by female philopatry and/or when males are not permanent group residents, but few studies have examined this possibility in male-dominant species so far. Overall, while new evidence indicates that intersexual dominance can be flexible and context-dependent, we know little regarding the extent and determinants of such variation, i.e. the ecology of intersexual dominance.

In this study, we investigate intersexual dominance relationships in mandrills (*Mandrillus*

sphinx). Mandrills are Old World primates living in large polygynandrous groups. They are seasonal breeders and most males enter the group at the onset of the mating season and leave afterwards, with only a few males remaining in the group during the birth season (Brockmeyer et al., 2015). Male-male competition is severe in this species (Setchell, 2016) and results in high reproductive skew, with 60-70% of reproductions monopolized by the alpha male (Charpentier et al., 2005; Charpentier et al., 2020). Mandrills exhibit extreme sexual size dimorphism: males are on average 3.4 times heavier than females (Setchell et al., 2001) while they display upper canines almost 5 times longer than females (Leigh et al., 2008). Male mandrills attain adult size and mass and show a major increase in mounts of fully swollen females (likely to be fertile) around the age of 9-10 years (Setchell et al., 2001). Their dominance rank increases with age, peaks from 11 to 16 (likely to be in their prime) and falls again after 16 years (Setchell, Wickings, and Knapp, 2006). Adult males are sexually coercive (Smit et al., 2022) and mate-guard females when they display maximally turgescient sexual swellings around ovulation (Setchell, Charpentier, and Wickings, 2005a). Females are philopatric and form differentiated social bonds and linear matrilineal hierarchies, with maternally inherited ranks that are relatively stable across their lives (Setchell et al., 2002). Despite large power asymmetries between sexes in mandrills, females can form coalitions against males, sometimes exceptionally violent (Setchell, Knapp, and Wickings, 2006).

Given these biological characteristics, we expect that some female mandrills may outrank some males. In a first step, we investigate the dynamics of intersexual dominance in mandrills at the “population level”, indexed by the percentage of males outranked by an average female in consecutive 6-month time blocks over an 8-year study period. We build intersexual dominance matrices using only dyadic decided interactions (i.e. one opponent exhibited submission) and we compute dominance hierarchies based on (i) all submissive behaviors (whether or not they follow aggression) and (ii) ritualized submissive behaviors only (in the absence of aggression), to test if intersexual dominance varies across behavioral contexts. We predict females to outrank less males when the social hierarchy is computed based on ritualized submissive interactions only, compared to a dataset comprising aggressive interactions occurring during conflicts. In a second step, we investigate factors that could influence the probability that a given female outranks a given male. We expect that (i) intrasexual dominance rank position predicts the posi-

tion of an individual in the intersexual hierarchy, (ii) females outrank more males during the mating season, when they are sexually receptive, thus have more leverage, and when the group includes more males, (iii) more socially integrated individuals are more dominant over the other sex as they have more social support, (iv) resident males (vs. immigrant ones) are better integrated thus more dominant over females and (v) females have a higher probability to outrank males who are not in their prime (the age range when males are strongest). In a final step, we investigate factors that may influence the probability of a female to win an intersexual conflict. We predict that (i) the greater the rank difference between the opponents (i.e. the more dominant the male and the more subordinate the female) the lower the probability for the female to win, (ii) sexually receptive females outrank more males than females in other reproductive states, given that they have more sex-related leverage, and (iii) females have a higher probability to win conflicts against males who are not in their prime.

1.2 Methods

Study System

We studied a natural population of mandrills living in a private park located in Southern Gabon. The population was established in 2002 after the release of 36 captive individuals initially housed in CIRMF (Centre International de Recherches Médicales de Franceville, Gabon). Another 29 individuals were released in 2006 (Peignot et al., 2008; Charpentier et al., 2020). Wild male mandrills were observed to join the group to reproduce, starting in 2003. A field research project (Mandrillus Project) was set-up in early 2012 to monitor the ecology, life-history and behavior of the population. Only 6 adult females out of 230 individuals (from which 79 were adult females) of the group were captive-born in late 2021. All the individuals of the population are individually recognized and daily censused.

We used behavioral, demographic and life-history data collected from April 2013 to September 2021 on 93 adult females (aged 4 yrs and older) and 35 subadult and adult males (aged 9 yrs and older). When the exact birth date was not known or approximated to a few days,

we estimated it using body condition and patterns of tooth eruption and wear (Galbany et al., 2014).

We divided the study period in 6-month time blocks roughly equating to the mating (April-September) and birth (October-March) seasons (Dezeure, Charpentier, and Huchard, 2022). When an individual turned adult during a season (6-month time block), we included it for the whole season.

We calculated a monthly group sex ratio (SR) as the number of adult females present in the group divided by the number of subadult and adult males that were censused in the group that month for at least a day. We also calculated the mean SR of each 6-month time block. Because the number of males largely varies between the mating vs. the birth season, season (birth vs mating) and group sex-ratio are correlated (Spearman's rank correlation: $\rho=0.59$, $p\text{-value}=0.02$) and we thus used these two effects in alternative models.

For each 6-month time block, we retrieved a male's "familiarity status" with the group, which we considered as a binary variable: "1" if the male was censused for first time in the group during the current time block and "0" otherwise.

Behavioral data

Behavioral sampling

Behavioral observations were made by observers blind to the focus of this study. We considered only dyadic interactions between adult females and adult or subadult males. *Ad libitum* observations and 5-min focal sampling (Altmann, 1974) were performed daily by recording, inter alia, affiliative and agonistic interactions between group members. In this study, we used four submissive behaviors (avoidance, displacement, escape and submissive vocalization) and we calculated intra- and intersexual hierarchies based on two different datasets: a "full dataset" that comprised all submissive interactions (which were preceded by an aggressive event, or not) and a "ritualized dataset" that included only those interactions that were not preceded by an aggressive event. These two datasets al-

lowed to test for potential discrepancies in dominance hierarchies due to methodological differences. We, however, did not use “undecided” aggressive interactions, i.e. those that were not followed by a submissive event, and which may not capture intersexual dominance relationships accurately.

Behavioral dataset

We considered a total of 2,768 hours (40,678 focal observations) of focal data in addition to ad libitum observations. For the analyses based on the full dataset, we used interactions from both focal and ad libitum observations to increase our sample size. In the ritualized dataset, we used only interactions from focal observations to filter out submissive behavior that followed an aggressive event. In the linear regression models performed below, we used only the full dataset given the similarity of the results based on these two different datasets (see results). For the analysis of intersexual conflicts, we selected from the full dataset all the dyadic interactions between an adult female and an adult male, recorded during focal observations, for which the outcome was unambiguous, i.e. when only one of the two individuals exhibited an aggression (mild threats were not included) followed by a submission from the other individual.

Dominance hierarchies

We used the functions *DS* and *ISIRanks* from the R package *EloRating* (Neumann et al., 2011) to compute the intersexual hierarchies with both normalized David’s score (David, 1987) and I&SI (de Vries, 1998) to evaluate whether these two rank estimates yielded different results suggesting potential methodological biases. David’s score is calculated for each individual based on the interactions this individual loses (i.e. submits to the opponent) or wins (i.e. the opponent submits) over other groupmates. As such, the difference among two individuals’ scores is more informative than the difference between their ordinal ranks, and reflects the extent of asymmetry in dominance-based power between these individuals. However, David’s score may be sensitive to missing data (non-interacting dyads; Neumann et al., 2011). On the other hand, I&SI generates the most parsimonious ordinal rank based on multiple randomizations (N=5,000) that re-order individual ranks

from an interaction matrix. Due to this iterative process, the resulting order may include more than one “solution” in the form of several equally likely rank orders. Whenever needed, we averaged the rank of each individual across these equally likely solutions. Finally, due to the randomization process, whenever we re-ran the algorithm, the resulting hierarchy could be slightly different. Due to the high level of correlation between David’s scores and I&SI within (see results) and across species (Kappeler et al., in press) and the greater stability of hierarchies based on David’s scores (Sánchez-Tójar, Schroeder, and Farine, 2018), we used normalized David’s scores (David, 1987) for downstream analyses.

Social integration and affiliation rates

During focal samplings, grooming events and their duration were recorded. For each 6-month time block, we used the total time of grooming recorded among females to create a female-only grooming directed network (function *graph_from_data_frame* from the package *igraph*; Csardi and Nepusz, 2006). We calculated the in-degree of each female from the above networks, as a proxy of social integration and support. We used only the number of females grooming (and not groomed by) a female, because we consider these individuals more likely to offer their support during agonistic interactions. Similarly, we calculated the total (in and out) degree of each male in networks including only intersexual grooming interactions (number of females grooming or being groomed by each male). For males, we considered all (given and received) grooming interactions in order to capture better male integration with the females of the group, rather than female support to males.

Reproductive state

The reproductive state of each adult female was determined on a near-daily basis based on sexual swelling size (scaled from 0 to 3 by increments of 0.5) and patterns of gestation and lactation. During an estrous cycle of a female mandrill, the perineal swelling inflates for some days and reaches maximal swelling size around ovulation where it remains maximal for a few days before deflating. Each female was classified as: “non-swollen” (i.e. non-fertile phase of the cycle that does not fall within the following three categories),

“swollen” (i.e. exhibiting an inflating or maximal perineal sexual swelling), “pregnant” (i.e. exhibiting a characteristic pregnancy swelling and/or if the female gave birth less than 163-190 days after a given day; average gestation length: mean \pm SD: 175.0 \pm 4.7 days; Dezeure, Charpentier, and Huchard, 2022) or “lactating” (i.e. nursing a \leq 6 month-old infant, without having resumed cycling).

Statistical Analyses

First, at the level of the population, we ran a Spearman’s rank correlation test to study whether the intersexual hierarchy differed when using either David’s score or I&SI. We then compared the percentage of males dominated by an average female in the two datasets (including all submissive interactions versus only ritualized submissive interactions) using a Spearman’s rank correlation test.

Second, at the dyad level, we ran a generalized linear model (GLMM) with a binomial distribution and a logit function to test whether the probability of a given female to outrank a given male was influenced by the following fixed factors: female and male intrasexual rank and ages, female’s in-degree in the female-only social network and its corresponding quadratic term (suggested following a graphical exploration of the data), and male’s total (in and out) degree in the social network including only intersexual grooming interactions, either season or sex ratio, and male’s familiarity. Female, male and dyad identity and the year were fitted as random factors.

Third, at the interaction (conflict) level, we ran a GLMM with a binomial distribution and a logit function to test whether the probability to win an intersexual conflict (1/0; response variable) for a given female was influenced by the following fixed factors: the rank difference between opponents (male and female David’s scores in the intersexual hierarchy), the age of the female, the age of the male and the corresponding quadratic term and female’s reproductive state. The female, male and dyad identity and the year were fitted as random factors.

We ran the above tests and models in R version 4.0.3 with the functions *cor.test* of the package *stats* and *glmmTMB* from the package *glmmTMB* (Brooks et al., 2017). We used

the *Anova* function of the package *car* (Fox and Weisberg, 2019) to test the significance of all fixed factors and we computed their 95% confidence intervals. We used the performed correlation tests to detect potential multicollinearities and we validated the performed models using the package *DHARMA* (Hartig, 2022).

1.3 Results

We found that female mandrills can outrank males, with a female outranking, on average, 11.3 ± 6.2 % (\pm SD; results based on the full dataset and David’s score or 18.2 ± 8.1 % based on I&SI) of males. We found a positive correlation between David’s score and I&SI metrics (Spearman’s rank correlation, $\rho=0.53$, p -value=0.03; see also: Kappeler et al., in press). This correlation, despite the low stability of the I&SI hierarchy which changed at each new calculation due to the stochastic component of its algorithm, suggests that our finding that adult female mandrills outrank some adult males is not an artifact.

Table 1.1: Factors affecting the probability for a female to outrank a male (Number of observations: 5,640 dyad.seasons). Random factors: 8 years; 93 females; 34 males; 1,893 dyads. Significant p -values and confidence intervals that did not cross zero appear in bold. The significance of each variable was assessed using chi-square tests (Chisq), while the significance of each level of a categorical variable was evaluated against a reference level (noted ‘Ref’) according to whether their confidence intervals (CI) overlap or not.

(a) Response variable: Probability to outrank a male (0/1)				
Fixed Factor	Estimate	CI 95%	Chisq	P-value
Female rank	0.280	[0.246;0.314]	260.060	<0.001
Male rank	-0.532	[-0.655;-0.409]	71.713	<0.001
Female degree	-5.221	[-18.650;8.208]	9.091	0.446
Female degree ²	17.692	[6.187;29.197]		0.003
Male degree	-0.634	[-0.739;-0.529]	140.421	<0.001
Season (Ref: Birth)	0.929	[0.538;1.320]	21.666	<0.001
Male familiarity	0.062	[-0.598;0.723]	0.034	0.854
Female Age	-0.037	[-0.096;0.021]	1.570	0.210
Male Age	53.565	[13.200;93.929]	21.752	0.009
Male Age ²	40.786	[17.604;63.967]		0.001

We found a strong positive correlation on the average number of males dominated by a female when using all submissive interactions and when using only ritualized submissive

interactions to build the intersexual hierarchy (Spearman's rank correlation, $\rho=0.72$, $p\text{-value}=0.001$ when we used David's score). When we used only ritualized submissive interactions to build the intersexual hierarchy, a female appeared to outrank, on average, $9.3\pm 5.1\%$ ($\pm\text{SD}$; results based on the David's score; see previous paragraph for the results based on the full dataset) of males.

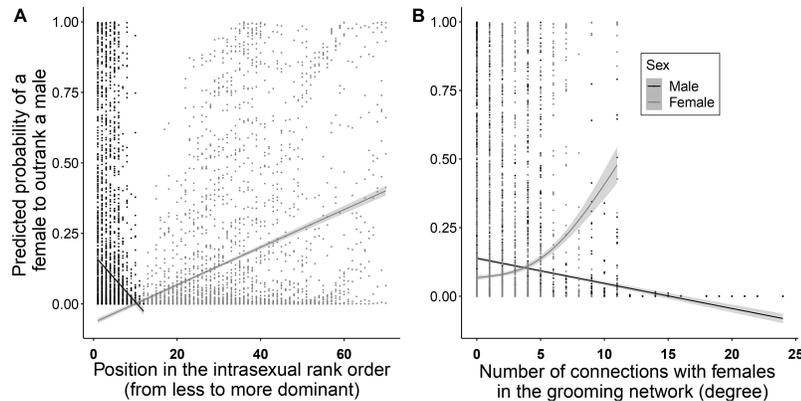


Figure 1.1: Factors influencing the probability for a female to outrank a male as a function of the (A) female (grey) and male (black) intrasexual rank (order/position in the intrasexual hierarchy; more dominant individuals have higher order) and (B) female (grey) and male (black) number of connections (degree for males and in-degree for females) in the grooming networks. The fitted values of the GLMM are shown on the y-axis and shaded areas show 95% confidence intervals.

A given female had a significantly higher probability to outrank a male when she was high-ranking and when he was low-ranking, in comparison to any other combination of rank-sex class (Figure 3.1A; Table 2.1). The probability for a female to outrank a male was significantly higher when male degree (number of female grooming partners) was lower (Figure 3.1B) and female in-degree (number of female partners grooming her) was higher although this relationship was not linear (Figure 3.1B; Table 2.1), suggesting that females need at least a certain number of female partners in order to have higher chances to outrank a male. In addition, a female had a higher probability to outrank a male during the mating (than birth) season (Table 2.1) or when group sex ratio was smaller (i.e., when there were less females in relation to males in the group; $\text{Chisq}=17.8427$, $p\text{-value}<0.001$). Female age was not significant but a female had a higher probability to outrank younger and older males than males in their prime (Figure 3.2; Table 3.1). Male familiarity did not

Table 1.2: Factors affecting the probability for a female to win a conflict against a male (Number of intersexual conflicts: 382). Random factors: 8 years; 41 females; 20 males; 182 dyads. Significant p-values and confidence intervals that did not cross zero appear in bold. The significance of each variable was assessed using chi-square tests (Chisq), while the significance of each level of a categorical variable was evaluated against a reference level (noted 'Ref') according to whether their confidence intervals (CI) overlap or not.

(b) Response variable: Probability to win an inter-sexual conflict (0/1)					
Fixed Factor	Level	Estimate	CI 95%	Chisq	P-value
Rank Difference		-23.333	[-49.563;2.897]	3.040	0.081
Reproductive State	Swollen (Ref: Non-Swollen)	17.167	[-17.347;51.682]	1.281	0.734
	Pregnant (Ref: Non-Swollen)	6.661	[-14.758;28.080]		
	Lactating (Ref: Non-Swollen)	9.501	[-18.957;37.959]		
	Pregnant (Ref: Swollen)	-6.086	[-27.915;15.743]		
	Lactating (Ref: Swollen)	-2.370	[-29.530;24.790]		
	Lactating (Ref: Pregnant)	5.914	[-51.749;63.577]		
Male Age		-173.450	[-309.137;-37.763]	7.324	0.012
Male Age ²		103.888	[-17.220;224.996]	7.324	0.093
Female Age		0.342	[-1.274;1.958]	0.172	0.678

influence the results.

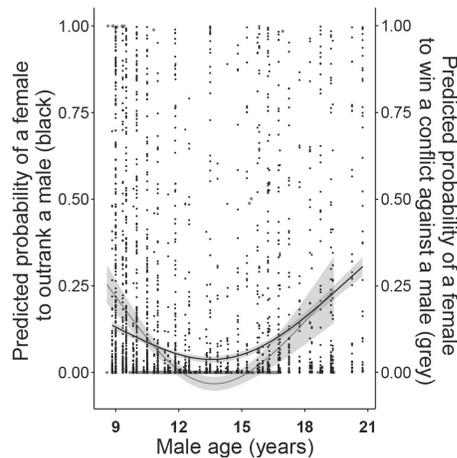


Figure 1.2: Male age in relation to the probability for a female to outrank a male (black) and win a conflict against a male (grey). The fitted values of the GLMMs are shown on the y-axes and shaded areas show 95% confidence intervals. For graphical purposes the quadratic term of male age is shown, although its effect on the probability to win an intersexual conflict was marginally non-significant (p-value=0.093).

The probability for a given female to win a conflict (only 11 out of 382 intersexual conflicts

were won by females) against a given male was higher for younger males than for males in their prime and tended to increase again when the male was older (marginally non-significant effect of the quadratic term; Figure 3.2; Table 2.2). In addition, a female tended to win more intersexual conflicts when the rank difference of the heterosexual dyad in the intersexual hierarchy was small (marginally non-significant effect; Table 2.2). Female age and reproductive state did not influence the results.

1.4 Discussion

In this study, we show that adult female mandrills can outrank some adult males despite being much smaller than them and traditionally considered strictly dominated by males. We show that intersexual dominance is not sensitive to the behavioral dataset used to construct the hierarchy since the percentages of males outranked by an average female when we used all submissive interactions (occurring across various contexts including conflicts) and when we used only ritualized submissive interactions (occurring in routine, outside conflicts) were correlated. We found that for both sexes, the intrasexual rank predicts the intersexual rank, suggesting that the intersexual hierarchy represents an interdigitation of the male and female intrasexual hierarchies. Furthermore, we show that the intersexual hierarchy is sensitive to seasonal changes, most likely due to demographic fluctuations in the group composition, and that individuals of both sexes can rise in the intersexual hierarchy by strengthening their social bonds with females of the group. Finally, although our sample size was small (only 11 out of 382 intersexual conflicts were won by females), our results indicate that a female has likely fewer chances to win a conflict against a male the largest their rank difference (the more dominant the male and the more subordinate the female; marginally non-significant effect) and when the male is young or old (marginally non-significant effect), suggesting that the outcome of such conflicts was predicted by opponents' asymmetry in force and power.

Male-biased sexual size dimorphism is generally associated with male-biased power (Kappeler, 1993) while female-biased dominance is more common in species with sexual size monomorphism (e.g. spotted hyenas: Vullioud et al., 2019; marmosets (*Callithrix flaviceps*: Ferrari, 2009; and lemurs: Petty and Drea, 2015). In the *Papio* species constellation,

which is phylogenetically close to mandrills and exhibits similar matrilineal polygynandrous groups, adult males often dominate most females, and can even be strictly dominant over them, as in chacma baboons (Kalbitzer et al., 2015). This raises the question of why sexual asymmetries in dominance appear less pronounced in mandrills, who are more dimorphic and also sexually coercive (Smit et al., 2022). In contrast to most baboon species, mandrills are seasonal breeders and a large proportion of males are not permanent resident in a group but enter the group at the onset of the mating season. Immigrant males are therefore not fully socially integrated during the mating season and may take some time to enter the intersexual hierarchy. Similarly, during the birth season, those males who stay in the group may have little incentive to trigger or join intersexual agonistic interactions. In line with this, several studies indicate that, in some social primates where males are not permanent group residents as in mandrills, intersexual conflicts are rare because males may avoid them and female residents win a large proportion of these conflicts (e.g. *Erythrocebus patas*; Hall, 1966; Goldman and Loy, 1997). Even if males remain largely dominant over females in the mandrill society, these results contribute to a new body of evidence that draws a more dynamic landscape of male-female power relationships (Surbeck and Hohmann, 2013; Young et al., 2017; Lewis, 2018; Davidian et al., 2022) where intersexual dominance is not (i) strictly biased towards males or females but varies along the full spectrum nor (ii) a fixed attribute of a species but can fluctuate across time and contexts.

Seasonal changes in intersexual dominance have already been documented and may be related to changes in individual reproductive states and associated needs (Jawor, 2000; Murie and Harris, 1988), motivation or leverage (Lewis, 2002; Lewis, 2018; Davidian et al., 2022). In particular, in species where females have some degree of reproductive control (i.e. control over when, and with whom to mate), they typically have more leverage when they are sexually receptive, such as in some lemurs (Hohenbrink et al., 2016; Lewis, Bueno, and Di Fiore, in press), because males who try to mate with them may avoid assaulting them (Lewis, 2002; Davidian et al., 2022). However, in contrast to such patterns and our prediction, we observe that sexually receptive female mandrills are not more likely to win conflicts against males in comparison to females in other reproductive states. Several reasons may explain such finding. First, these analyses suffer from low statistical power and caution is needed when interpreting these results. Second, in-

creased sex-based leverage by females only occurs when females have some degree of reproductive control, meaning that males cannot coerce sex and must trade it instead (Lewis, 2002; Lewis, 2018; Davidian et al., 2022). Mandrill females likely have low reproductive control, as they face sexual coercion from males (Smit et al., 2022), meaning that they may not gain any leverage from being receptive, and instead face more aggression from males. Third, shifts in intersexual power may further reflect motivational shifts in males and females across contexts. For females, the relative benefits of winning intersexual conflicts are likely higher in the birth season, when they have higher energetic demands due to the physiological costs of lactation (Dunham, 2008), as well as an infant to protect against infanticidal threats. Likewise, female Columbian ground squirrels (*Spermophilus columbianus*) become more dominant over males during lactation when they have higher energetic needs (Murie and Harris, 1988). In accordance with these results, female mandrills direct four times more aggression towards males during the birth (0.004 ± 0.004) than during the mating (0.001 ± 0.002 number per hour) season, and similar patterns have also been observed in other social primates (eg. Japanese macaques (*Macaca fuscata*): Schino, D'Amato, and Troisi, 2004; and humans: Hahn-Holbrook et al., 2011).

Female mandrills appeared, however, more likely to outrank males during the mating (vs. birth) season. The observed seasonal differences in intersexual dominance may reflect demographic changes in the composition of the group rather than contextual changes. The seasonal immigration of male mandrills in the group during the mating season may explain, at least partially, the flexibility of intersexual dominance across seasons. In line with such explanation, when there are more males in the group (in relation to females) the probability for a female to outrank a male is higher (see results on sex ratio). Recent studies on other primates have demonstrated that when the proportion of males in a group is higher, females are dominant over more males (Hemelrijk, Wantia, and Isler, 2008; Hemelrijk et al., 2020) due to 'winner and loser effects' (see introduction), an effect potentially reflected by our results. Yet, such an effect is only plausible during the mating season, when male-male competition is fierce and leads to male-male fights, while the absence of male-male fights in the birth season could not give rise to such effect. Alternatively or additionally, an increase in the number of males may lead them to adopt different reproductive strategies. In other mammals, when many males

are present, older males or males with lower competitive abilities engage less in mating-related activities and focus on the development of affiliative relationships with females and/ or offspring care to gain mating opportunities (Mysterud et al., 2003; Van Schaik and Paul, 1996; Silk et al., 2020). It is possible that male mandrills may adopt alternative mating strategies, as in rock hyraxes (Bar Ziv et al., 2016), where high-ranking resident males may compete to mate-guard ovulatory females, while lower-ranking immigrants may remain more peripheral and try to get sneaky matings with females. Finally such males may develop affiliative relationships or friendships with females and may assault females less and mitigate their motivation to interact agonistically with them.

In this study, we show that male mandrills were less dominant in the intersexual hierarchy when they had less female grooming partners, i.e. when they were more peripheral or less socially integrated. This result may further indicate that those males who take an active part to the social dynamics of the group simultaneously rise in rank, while females often outrank young, old or peripheral males who may lack motivation to trigger or win conflicts with females or rivals. Such an interpretation is strengthened by our results showing that females outrank or win more conflicts against young or old males than against males in their prime. Similarly, young male chimpanzees which are physically and socially immature may be unable to direct aggression to females as effectively as older males (Reddy and Mitani, 2020). An alternative interpretation is that female mandrills can control, to some extent, male social integration which subsequently helps males to rise in the social hierarchy. Studies on vervet monkeys have shown that females can influence a male's intrasexual rank through affiliative intersexual interactions (Young et al., 2017). Although female mandrills, in comparison to female vervets, seem to have relatively less reproductive control (Smit et al., 2022), our results suggest that female-dependent social integration ('social control') in mandrills is beneficial to the rise in intersexual hierarchy for individuals of both sexes. In line with this result, female mandrills can form aggressive coalitions against males (Setchell, Knapp, and Wickings, 2006; NS personal observation) which altogether may suggest that such coalitions can help females to dominate males, similarly to other species (spotted hyenas: Vullioud et al., 2019; bonobos: Parish, De Waal, and Haig, 2000).

This study adds to a growing body of evidence showing that intersexual dominance can

vary along a spectrum from strict male to strict female dominance. We report here evidence that females occasionally dominate some males in a highly dimorphic nonhuman primate where males are sexually coercive, and generally dominate females. Although females outrank more males in the mating season, our results suggest that they do not have higher chances to win conflicts against them when they are sexually receptive, confirming that they have low reproductive control and associated leverage, as such leverage typically translates into greater dominance in sexually receptive females (Lewis, 2002; Davidian et al., 2022). Moreover, females who were high-ranking and more socially integrated were dominant over more males; and they preferentially outranked males who were low-ranking, younger or older, thus with low competitive abilities, and poorly socially integrated. Similarly, females won more intersexual conflicts when they were high-ranking and interacted with low-ranking and young or old males. Altogether, these results point to the importance of social integration and seasonal breeding, and of associated demographic and motivational shifts in males and females, to explain the dynamics of intersexual dominance. Further research should shed light on the potential effects – or lack thereof - of such female empowerment on mate choice patterns by testing if females who dominate more males are better able to express mate choice, or less vulnerable to coercion or infanticide, at least from those males they outrank. This study is opening a new area aimed at understanding the dynamics of male-female power struggles from a population to an individual scale, as well as its evolutionary consequences.

Competing interests: The authors declare no competing interests.

Ethics: This study was approved by an authorization from the CENAREST institute (permit number, AR0060/18/MESRS/CENAREST/CG/CST/CSAR) and followed all applicable international, national, and/or institutional guidelines for the care and use of animals.

Data accessibility: The datasets and scripts necessary to replicate analyses included in this manuscript can be found in the public depository <https://gitlab.com/nksmt/mandrills2>.

Authors' Contributions: E.H., N.S. and M.J.E.C. designed the study; N.S performed the statistical analyses and wrote the first version of the manuscript; E.H., N.S. and M.J.E.C. contributed to writing the manuscript; M.J.E.C., B.N. and N.S. contributed to data collection and database management.

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Chapter 2

Sexual coercion in a natural mandrill population

Authors

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Abstract

Increasing evidence indicates that sexual coercion is widespread. While some coercive strategies are conspicuous, such as forced copulation or sexual harassment, less is known about the ecology and evolution of intimidation, where repeated male aggression promotes future rather than immediate mating success with targeted females. Although known in humans, intimidation was recently reported in chimpanzees (*Pan troglodytes*) and chacma baboons (*Papio ursinus*), where males are regularly violent against females. Here, we investigate the nature of male coercive strategies in wild mandrills (*Mandrillus sphinx*), a primate living in large polygynandrous groups where severe male aggression towards females is rare and females can form coalitions against males. Yet, we found support for all three predictions of the sexual coercion hypothesis, namely that male aggression (1) specifically targets sexually receptive females, (2) inflicts costs to these females, and (3) increases male mating success in the long-term. These results hold true when considering only non-physical threats, or only severe aggression. Finally, we show that high-ranking females are most targeted by males, probably because of their higher reproductive performances, while high-ranking males are most coercive. These results indicate that sexual intimidation is widespread in sexually dimorphic and group-living mammals, and that males and females vary in their propensities to use, and to be exposed to sexual coercion, respectively.

2.1 Introduction

The diverging evolutionary interests of males and females often lead to sexual conflict. While female reproductive success is typically limited by the elevated costs of reproduction, e.g. gestation and lactation in mammals, male reproductive success is primarily determined by the number of mating partners (Bateman, 1948). In some species, males use sexual coercion towards females, defined as “the use by a male of force, or threat of force, that functions to increase the chances that a female will mate with him at a time when she is likely to be fertile, and to decrease the chances that she will mate with other males, at some cost to the female” (Smuts and Smuts, 1993), to improve their mating

success (Smuts and Smuts, 1993; Clutton-Brock and Parker, 1995b).

Behavioural ecologists have traditionally documented coercive strategies that are immediately visible, such as forced copulation (when a female is physically restrained by a male to mate with him), sexual harassment (when aggression immediately precedes copulation and is directed until the female cedes; Smuts and Smuts, 1993) and coercive mate-guarding (when a male aggressively herds females and enforces close proximity to prevent them to copulate with rival males; Muller et al., 2011; King et al., 2019). These forms of sexual coercion have been reported from insects (Arnqvist, 1989; Parker, 1979) to vertebrates (Head and Brooks, 2006; Bro-Jørgensen, 2011; McKinney and Everts, 1998; Galdikas, 1985; Connor and Vollmer, 2009). In contrast, long-term forms of sexual coercion – when aggression does not translate immediately but subsequently into mating benefits for the aggressor – are more elusive and have been less studied outside of human societies. Sexual intimidation, when repeated male aggression aims at enforcing future female sexual compliance, has only been documented in two primate societies characterized by severe male aggression to females (chimpanzees (*Pan troglodytes*): Muller et al., 2007; chacma baboons (*Papio ursinus*): Baniel, Cowlshaw, and Huchard, 2017). Similarly, males of different taxa (e.g. birds and primates including humans) can also punish females following copulation with rival males to prevent cuckoldry in the future (Clutton-Brock and Parker, 1995a; Valera, Hoi, and Krištín, 2003; le Roux et al., 2013; Rodseth and Novak, 2009).

Sexual coercion is increasingly recognised as a driving force influencing the evolution of mating and social systems in animals (Thornhill, Alcock, et al., 1983; Smuts and Smuts, 1993; Clutton-Brock, 2021), including humans (Smuts, 1992; Stumpf et al., 2011). In mammals, male coercive tactics appear most common in polygynous and polygynandrous species where males compete intensively over mating opportunities and a substantial fraction of males fails to secure mating, and where sexual size dimorphism is pronounced, allowing males to threaten or harass females at low costs (Nunn and van Schaik, 2000; Cassini, 2021). In these species, female impediment to male copulation attempts has been associated with an increased risk of severe injury or even death (Cassini, 2000). The forms of coercion used by males are then likely to vary according to the stability of male-female associations and male dominance status. Short-term strategies such as sexual ha-

harassment and forced copulation may be frequently used in solitary species, where males and females only encounter each other for mating (Clutton-Brock and Parker, 1995b). By contrast, long-term strategies, such as intimidation and punishment, are more likely to evolve in species living in stable bisexual groups where males and females maintain medium- to long-term social relationships. Furthermore, in polygynous groups, harassment and forced copulation might be used more frequently by subordinate males that are excluded from mating opportunities (Boeuf and Mesnick, 1991; Kunz et al., 2021b) while long-term male coercive strategies might be used more often by dominant males to constrain female promiscuity and impose closer proximity (e.g. Swedell and Schreier, 2009).

Primates are good candidates to study sexual coercion because the diversity of their social and mating systems may promote various male and female sexual strategies, while their extensive cognitive abilities, including individual recognition and long-term memory, may facilitate the use of long-term male coercive strategies (Stumpf et al., 2011). Such strategies are also promoted by the fact that many primates live in stable bisexual groups where males and females maintain differentiated relationships, and by a widespread male-biased sexual dimorphism associated with polygynous or some polygynandrous mating systems.

In this study, we examine whether males exert sexual coercion in a large natural, polygynandrous group of mandrills (*Mandrillus sphinx*), a primate from the *Cercopithecidae* family characterised by an extreme sexual dimorphism in body size (males are 3.4 times heavier than females; Setchell et al., 2001) and canine length (Leigh et al., 2008). Mandrills are seasonal breeders and most males immigrate in the social group at the onset of the mating season (Brockmeyer et al., 2015; which generally lasts every year from April to September; Dezeure, Charpentier, and Huchard, 2022), resulting in intense male-male mating competition (Setchell, 2016). Male reproductive skew is high, since the alpha male monopolises 60-70% of reproductions (Charpentier et al., 2020; Charpentier et al., 2005). Female mandrills develop perineal swellings during fertility that grow in size as they approach ovulation and dominant males focus their mate-guarding efforts on maximally swollen females (Setchell, Charpentier, and Wickings, 2005a). Yet, both sexes mate promiscuously and females may exhibit some forms of mate choice (Setchell, 2005), for

example by avoiding males' attempts to copulate or interrupting copulation before ejaculation (MJEC personal observation). Severe male aggression towards females occurs but appears relatively infrequent for human observers. Female relatives form tight social relationships (Charpentier et al., 2020), including aggressive coalitions against males that can, exceptionally, lead to male's death (in captivity: Setchell, Knapp, and Wickings, 2006). Studying male sexual coercion in this species, where most males are temporary residents in the group during the mating season, females can retaliate against males and severe male aggression against females is inconspicuous, appears thus highly relevant.

We test the three key predictions of the sexual coercion hypothesis (Smuts and Smuts, 1993), namely that male aggression (i) targets sexually receptive females more than females in other reproductive states, (ii) is costly to females in the form of a greater exposure to injuries, and (iii) increases male mating success with the victim. For this last prediction, we further investigate different forms of coercion by testing if aggression by a male towards a female increases his chances to mate with her within the following minutes (harassment) or within a longer time-window (intimidation). We also test whether a female that has just copulated with a given male receives immediate aggression from other male(s) as a punishment. We subsequently test whether higher-ranking males are more aggressive towards females during the mating season given the high reproductive skew in their favour. Finally, as an alternative hypothesis to sexual coercion, we test the "aggressive male phenotype" hypothesis, stating that the correlation between male aggression and mating is observed because females prefer to copulate with aggressive males due to direct (e.g. better infanticide protection) or indirect (i.e. better genes for their offspring; Fisher, 1915) fitness benefits of these male traits to females (Cordero and Eberhard, 2003; Pizzari and Snook, 2003).

2.2 Methods

Study system

We studied a natural population of mandrills established in 2002 by the release of 36 captive individuals followed by the release of another 29 individuals in 2006, in the Lékédi

park, a private park located in Southern Gabon (Peignot et al., 2008). Starting in 2003, wild males joined the group to reproduce. In early 2012, the Mandrillus Project was set-up to study this population, benefiting from an initial habituation of these captive-born individuals to human presence. In early 2020, only 8 females from ca. 210 individuals were captive-born. All individuals were individually-recognised, daily monitored and censused.

Behavioural data

Trained observers, blind to the topic of this study, collected daily ad libitum behavioural observations and performed 5-min focal sampling on all study individuals (Altmann, 1974). In this study, we used 2182 hours of focal data collected on 81 adult females aged ≥ 4 yrs (mean \pm SD: 26.9 \pm 39.3h per female) and 670 hours collected on 34 subadult and adult males aged ≥ 9 yrs (19.7 \pm 29.2h per male), collected from August 2012 to March 2020. We included subadult males (aged 9-10 yrs) because they have usually reached their full adult body size (Setchell and Dixson, 2002) and have started competing with other males and mate with adult females (Setchell, Charpentier, and Wickings, 2005b). During focal sampling, sexual and agonistic interactions between a focal individual and its groupmates were recorded. The observers systematically recorded copulation of males with females (n=275). Male aggressive events towards females included grasping/hitting (n=401), biting (n=18), chasing (n=65), lunging (n=383), slapping the ground (n=138) and head bobbing (n=567). For the analyses below, we ran the models including all these behaviours and we also replicated the analyses using only severe aggression (grasping/hitting, biting and chasing) or only threats (lunging, slapping the ground and head bobbing) because both categories produce different female behavioural reactions (see discussion). Dominance ranks were established separately for each sex (on a yearly basis for females and on a monthly basis for males) based on avoidance and displacements and calculated using normalised David's score (David, 1987; as per Poirotte et al., 2017). Female rank is maternally inherited and generally stable during a female's life (Setchell et al., 2002). Here, females were divided into three classes of equal size (high-, medium- and low-ranking) while male rank was considered as a binary variable (alpha versus non-alpha) because of the distinct behavioural characteristics of the alpha male, who monopolises

most swollen females and is relentlessly challenged by other males (Charpentier et al., 2018). In the test for intimidation, in case the swollen period spanned over two consecutive months, a male was considered as alpha if he achieved the highest position for at least one of these two months.

Age and male immigration patterns

The exact date of birth was known for 25 individuals. For the remaining 90 individuals, the date of birth was estimated using body size, condition and patterns of tooth eruption and wear (Galbany et al., 2014). The error made when estimating the age of these 90 individuals was less than a year (50 individuals), two years (26 individuals), three years (13 individuals) or five years (1 individual). Long-term life-history and demographic data were also available from all individuals.

Census data allowed to reconstitute patterns of male residency in the group. Here, we considered a male as resident in a given mating season when censused in the group late during the preceding birth season, between January and March. When censused for the first time during the mating season (which takes place once per year between April and September) we considered the male as immigrant. For immigrant males, the first census date was the “arrival date”. Each year, the day of arrival of the first immigrant male in the group was considered as the onset of the mating season (Figure S1).

Female reproductive state and sex ratio

During each female oestrous cycle, the perineal swelling inflates for several days until reaching a maximal swelling size around ovulation. Swelling size remains maximal for a few days before deflating within a few days. We used a scale from 0 to 3 (by increments of 0.5) to evaluate the swelling size of each female on a near-daily basis. The reproductive state of each adult female was also recorded on a near-daily basis. Each female was classified as: “non-swollen” (i.e. non-fertile phase of the cycle that does not fall within the following three categories), “swollen” (i.e. with a perineal sexual swelling), “pregnant” (i.e. with a characteristic pregnancy swelling and/or if she gave birth 163-190 days

afterwards (average gestation length: mean \pm SD: 175.0 \pm 4.7 days; Dezeure, Charpentier, and Huchard, 2022) or “lactating” (i.e. nursing a \leq 6 month-old infant without having resumed cycling). Finally, females were considered as nulliparous until their first parturition, and parous afterwards. We calculated monthly adult group sex ratio (SR) or group operational sex ratio (OSR) as the number of females (for SR) or females with inflating sexual swelling or swelling of maximal size (for OSR) divided by the number of males aged 9 yrs and above that were censused in the group that month.

Injuries

We recorded the occurrence, type of wound, freshness and body location of any injury on a near-daily basis on all subjects (Dibakou et al., 2019). A total of 90 injuries (limping n=15, puncture of the skin n=11, bleeding or swollen skin n=48, other n=16) were recorded on 43 females over the study period. For most injuries, we did not witness the interaction and the cause but in the three cases with a known context the injury was inflicted by a male. We never observed violent female-female aggression resulting in an injury.

Statistical Analyses

To test whether male aggression targets swollen females preferentially (first prediction), we ran a binomial generalised linear mixed models (GLMMs) with a logit link function to study the relationship between the probability that a female received aggression by any (adult or subadult) male during that female focal observation (0/1; response variable) and her reproductive state at the time of observation (non-swollen, swollen, pregnant and lactating; for sample sizes, see table S1). We further controlled for the following fixed effects: female dominance rank (high-, medium- or low-ranking) to test if higher-ranking females are preferentially targeted by males, parity (nulliparous or parous) to test if parous females are preferentially targeted by males, SR to test if the number of males in relation to females in the group influences the probability of occurrence of male aggression and the duration of focal observation (\leq 5min) to control for the observation

time. Female identity and the year of focal observation were fitted as random factors. Second, we ran a similar model (same structure of fixed and random effects) with the response variable corresponding to the probability that a female received aggression by groupmates other than adult or subadult males. By doing so, we tested if swollen females were generally more targeted than any other female, regardless of the age-sex group of the aggressor.

To test whether swollen females were more injured than females in other states (second prediction), we ran a binomial GLMM with a logit link function to study the relationship between the probability that a female got injured (observed injured for first time) on a given day (0/1; response variable) and her reproductive state that same day. As above, we further controlled for the following variables: female dominance rank and parity, and SR. Female identity and the year of focal observation were fitted as random factors (table S1). The daily monitoring of the group allowed us to detect with accuracy the day of occurrence of each injury.

We then tested whether males who were more aggressive also had a higher mating probability with their victim (third prediction). To study intimidation, we performed a binomial GLMM with a logit link function to test whether the rate of aggression received by a female from a given male (continuous fixed effect) before the next oestrous cycle of the female increased the probability of copulation of that heterosexual dyad during the female's swollen period (0/1; response variable). The "aggression window" before the swollen period was defined as the time elapsed between the onset of the mating season (for resident males) or a male's arrival in the group a given year (for immigrant males) and until the beginning of the swollen period of the female (spanning from the first day of a female's sexual swelling to the last day where swelling size was maximal: mean \pm SD: 10.6 \pm 5.1 days; Figure S1). We pooled focal observations from females and males (table S1). We controlled for the following fixed effects in our model: female dominance rank and parity, OSR (since we focused only on swollen females for that prediction) in the month corresponding to the first day of maximal swelling, male dominance rank (alpha vs. non-alpha) that same month in interaction with the rate of male aggression (to test whether the aggression of alpha males had a greater impact on their mating success than the aggression of subordinate males) and the total focal observation time of the studied

heterosexual dyad (during the swollen period of the female) to control for the time of observation. Female identity, male identity and year of observation were fitted as random factors. We restricted our analyses to those heterosexual dyads that were observed for at least 30 minutes of focal time during the female swollen period to avoid biases due to under-sampling that would prevent us from estimating reliably mating probability. However, we validated that our results remained similar when we used slightly different thresholds (25 or 35 minutes) or no threshold at all. We further ran the same model but restricting the swollen period to the few days of the cycle during which the female was maximally swollen (i.e. where the probability of conception is the highest; mean \pm SD: 2.9 \pm 2.9 days). Finally, to test for immediate effects of male aggression, we ran the same model as above considering the rate of aggression received by a female from a given male during her swollen period only (Figure S1, top line).

To test for sexual harassment, we assessed for each female and male focal observation during which an aggressive event was recorded from a male to a swollen female, whether a copulation occurred or not between that same heterosexual dyad in the 150 seconds following the aggression (see electronic supplementary material; Figure S2). To test for male punishment, we assessed for each female and male focal observation during which a copulation event was recorded between a male and a swollen female, whether an aggression from a different male occurred towards the copulating female in the 150 following seconds (Figure S2; Table S1).

We further ran GLMM with a negative binomial distribution to test whether alpha males were more aggressive than subordinates during the mating season. We used as a response variable the number of aggression events a male directed towards all adult females during each month of the mating season (April to September). We considered only aggression towards females that were potential mating partners for males: late lactating females (during the 5th and 6th month of lactation when some females have already resumed cycling; MJEC personal observation), “non-swollen”, “swollen” and early pregnant females (during the first two months of pregnancy, since males may not be able to distinguish early pregnant from “non-swollen” females). We pooled focal observations from females and each given male (Table S1). We included the following explanatory variables: male dominance rank (alpha vs. non-alpha) and age (to test if younger males are more ag-

gressive) and the OSR (to test if males are more aggressive when there are few swollen females in comparison to the number of males in the group). The observation time of a given male and all the females was log-transformed, and fitted as an offset variable. Male identity and the year of observation were fitted as random factors.

We explored an alternative scenario to sexual coercion, the “aggressive male phenotype” hypothesis (Fisher, 1915; Huk and Winkel, 2007), to test whether males with aggressive phenotype have higher mating success than less aggressive males, potentially because aggression may act as a sexually selected trait and may be chosen by females. We reran the GLMM used for testing the occurrence of intimidation, including as an explanatory variable the overall rate of aggression directed by the focal male towards any groupmate (except for adult females) during the corresponding mating season.

We ran all the above statistical tests in R version 4.0.3. For generalised linear mixed models (GLMMs; summarised in Table S1) we used the *glmer* function of the *lme4* package (Bates et al., 2015; binomial models) and *glmmTMB* from the package *glmmTMB* (Brooks et al., 2017; negative binomial model). Whenever a singular fit was observed, we reran the relevant model with the *bglmer* function of the *blme* package (Chung et al., 2013). Whenever necessary we increased the number of iterations and/or we changed the optimiser of the model to achieve model convergence of the model and improve its fit. We used the *Anova* function of the *car* package (Fox and Weisberg, 2019) to test for the significance of fixed factors and computed their 95% confidence intervals. We further used the *vif* function of the same package to detect multicollinearities. All VIFs were <2.5 indicating no serious multicollinearities (Zuur, Ieno, and Elphick, 2010). For multilevel categorical factors such as reproductive state, we switched the reference category sequentially (Pinheiro and Bates, 2006) in order to test for pairwise differences between categories. We explored the distribution of residuals to validate the models using the functions *testDispersion* and *simulateResiduals* from the *DHARMA* package (Hartig, 2022).

2.3 Results

Prediction 1: Male aggression targets swollen females

Swollen females received significantly more aggression from males (mean±SD: 0.613±1.070 bouts per hour) than females in any other reproductive state (non-swollen: 0.331±0.661, pregnant: 0.309±0.528 and lactating: 0.288±0.562; Figure 3.1a; Table 2.1). Such pattern was found for both severe aggression (Chisq=12.539, p-value=0.006) and threats (Chisq=8.660, p-value=0.034). By contrast, swollen females were not significantly more targeted by other groupmates (Figure S3; Table S2). In addition, high-ranking females received more male aggression than lower-ranking females (high-ranking females: 0.461±0.328 bouts/hour, medium-ranking females: 0.216±0.240, low-ranking females: 0.148±0.149; Table 2.1).

Table 2.1: Male aggression in relation to female reproductive state (for sample sizes, see Table S1). Significant p-values and confidence intervals that did not cross zero appear in bold. The significance of each variable was assessed using chi-square tests (Chisq), while the significance of each level of a categorical variable was evaluated against a reference level (noted 'Ref') according to whether their confidence intervals (CI) overlap or not.

Response variable: Probability of receiving aggression from adult males (0/1)					
Fixed Factor	Level	Estimate	CI 95%	Chisq	P-value
Reproductive State	Swollen (Ref: Non-Swollen)	0.442	[0.170;0.714]	15.926	0.001
	Pregnant (Ref: Non-Swollen)	0.070	[-0.132;0.273]		
	Lactating (Ref: Non-Swollen)	-0.094	[-0.309;0.122]		
	Swollen (Ref: Lactating)	0.536	[0.268;0.804]		
	Pregnant (Ref: Lactating)	0.164	[-0.030;0.358]		
	Swollen (Ref: Pregnant)	0.372	[0.116;0.628]		
Female Rank	Low Rank (Ref: High Rank)	-0.718	[-0.981;-0.456]	31.124	<0.001
	Medium Rank (Ref: High Rank)	-0.554	[-0.904;-0.203]		
Female Parity	Parous (Ref: Nulliparous)	0.150	[-0.230;0.529]	0.599	0.439
Group Sex Ratio		-0.014	[-0.059;0.031]	0.375	0.540
Observation Time		-0.097	[-0.167;-0.027]	7.459	0.006

Table 2.2: Injuries in relation to female reproductive state (for sample sizes, see Table S1). Significant p-values and confidence intervals that did not cross zero appear in bold. The significance of each variable was assessed using chi-square tests (Chisq), while the significance of each level of a categorical variable was evaluated against a reference level (noted 'Ref') according to whether their confidence intervals (CI) overlap or not.

Response variable: Probability of having an injury (0/1)					
Fixed Factor	Level	Estimate	CI 95%	Chisq	P-value
Reproductive State	Swollen (Ref: Non-Swollen)	1.183	[0.579;1.787]	34.535	<0.001
	Pregnant (Ref: Non-Swollen)	-0.452	[-1.026;0.123]		
	Lactating (Ref: Non-Swollen)	-0.507	[-1.076;0.061]		
	Swollen (Ref: Lactating)	1.656	[1.013;2.299]		
	Pregnant (Ref: Lactating)	0.100	[-0.503;0.704]		
	Swollen (Ref: Pregnant)	1.556	[0.943;2.169]		
Female Rank	Low Rank (Ref: High Rank)	0.203	[-0.396;0.802]	2.812	0.245
	Medium Rank (Ref: High Rank)	-0.418	[-1.146;0.310]		
Female Parity	Parous (Ref: Nulliparous)	0.132	[-0.826;1.090]	0.073	0.787
Group Sex Ratio		-0.013	[-0.109;0.083]	0.071	0.789

Prediction 2: Swollen females are more injured

Swollen females were, on average, about five times more likely to become injured (mean±SD: 0.005±0.016 injuries per day) than females in any other reproductive state (non-swollen: 0.001±0.004, pregnant: 0.001±0.002 and lactating: 0.001±0.002; Figure 3.1b). None of the other fixed factors, including female rank, parity and the group sex-ratio were significantly correlated with the probability of injury (Table 2.2).

Prediction 3: Aggressive males have higher mating success with their victim

We found support for sexual intimidation in mandrills: the rate of male aggression received by a female during the time window preceding her swollen period (starting at the onset of a given mating season for resident males, or at male's arrival date in the group for immigrant males) was significantly and positively correlated to the probability of copulation of the dyad during that swollen period (Figure 3.1c; Table 2.3). In dyads with no male aggression, the average number of copulation per observation time was 0.09±0.24

(\pm SD). By comparison, dyads where the male assaulted the female e.g. at least 0.1 times per hour, the average number of copulation per observation time doubled (0.17 ± 0.45). Alpha males copulated more than subordinate males, while female rank, parity, OSR and the interaction between male rank and aggression ($\text{Chisq}=0.030$, $p\text{-value}=0.862$) were not significantly correlated with the probability of copulation (Table 2.3). The correlation between male aggression and mating within dyads remained significant when restricting the swollen period to the few days where a female was maximally swollen (i.e. close to ovulation, $\text{Chisq}=4.574$, $p\text{-value}=0.032$). However, the rate of male aggression calculated during the swollen period of the female (instead of before) did not significantly predict the probability of copulation during that same swollen period (Table S3a). This indicates that immediate aggression (i.e. during the swollen period) did not clearly influence female mating pattern, while previous aggressive interactions over a longer period (i.e. before the swollen period) did. The pattern of correlation between aggression and subsequent mating holds when only including severe aggression (Table S3b) and becomes marginally non-significant when only including threats (Table S3c). Note that the rate of severe aggression and the rate of threats a female receives from a male were moderately correlated (Kendall's tau=0.28, $p\text{-value}<0.001$).

Table 2.3: Male aggression and mating success (for sample sizes, see Table S1). Probability of copulation of a heterosexual dyad during a female's swollen period in relation to the rate of male aggression received before that swollen period. Significant p-values and confidence intervals that did not cross zero appear in bold. The significance of each variable was assessed using chi-square tests (Chisq), while the significance of each level of a categorical variable was evaluated against a reference level (noted 'Ref') according to whether their confidence intervals (CI) overlap or not.

Response variable: Mating during the swollen period (0/1)					
Fixed Factor	Level	Estimate	CI 95%	Chisq	P-value
Aggression Rate		1.591	[0.115;3.067]	4.466	0.035
Male Rank	Alpha (Ref: Non-alpha)	1.242	[0.490;1.994]	10.476	0.001
Female Rank	Low Rank (Ref: High Rank)	0.699	[-0.186;1.584]	2.664	0.264
	Medium Rank (Ref: High Rank)	0.715	[-0.645;2.075]		
Female Parity	Parous (Ref: Nulliparous)	-0.454	[-2.815;1.907]	0.142	0.706
Operational Sex Ratio		0.024	[-0.495;0.543]	0.008	0.928
Observation Time		0.548	[0.221;0.875]	10.807	0.001

We did not find support for sexual harassment and punishment. Following aggression, females copulated immediately (i.e. within 150 seconds) with their aggressor in only

three out of 38 total cases of aggression observed between a male and a swollen female. Similarly, males were never observed directing aggression to a female in the 150 seconds after she copulated with a rival male ($n=173$). Those sample sizes precluded any further formal statistical testing of those hypotheses.

Alpha males were significantly more aggressive towards adult females. Indeed, an alpha male assaulted, on average, about 2 times more adult females (mean \pm SD: 0.05 ± 0.07 bouts per hour) than a non-alpha male (0.03 ± 0.06 ; Figure S4; Table 2.4). In addition, males were more aggressive (marginally significant effect; Table 2.4) when there were more swollen females in the group in relation to males but male aggression did not depend on its age (Table 2.4).

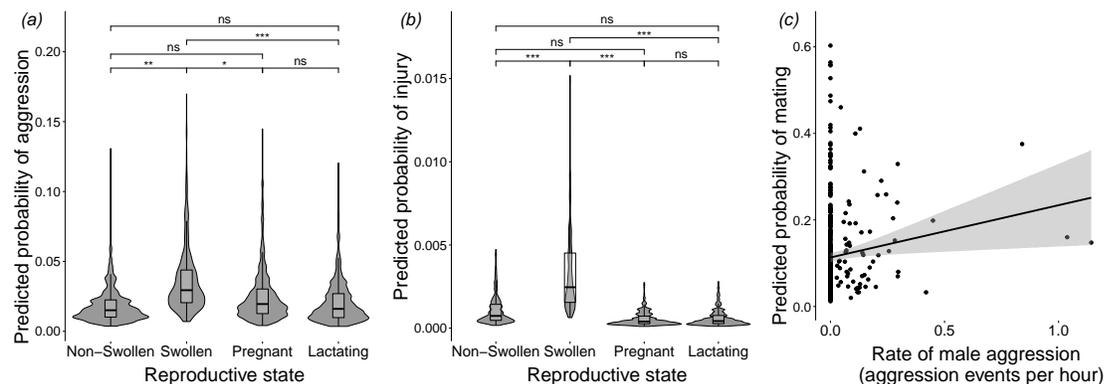


Figure 2.1: Results of the tests of the three predictions of the sexual coercion hypothesis. (a) Predicted probability of male aggression received by females as a function of their reproductive state. (b) Predicted probability for females to get injured as a function of their reproductive state. (c) Predicted probability of copulation of a heterosexual dyad as a function of male aggression rate (number of events per hour) received by the female before her swollen period. The fitted values of the GLMMs are shown on the y-axes. In a and b, the violin plots show the predicted probabilities while pairwise comparisons across female reproductive states with corresponding p-values are shown. ‘ns’: not significant ($p>0.05$); *: $p<0.05$; **: $p<0.01$; ***: $p<0.001$. In c, for graphical purposes, the regression line is simple linear fit and the shaded area shows the 95% confidence intervals.

Lastly, we did not find evidence for a female preference for aggressive male phenotype, as females were not more likely to mate with the most aggressive males of the group (see electronic supplementary material).

Table 2.4: Male rank and aggression (for sample sizes, see Table S1). Male aggression towards adult females in the months of the mating season in relation to male rank, age and sex ratio. Significant p-values and confidence intervals that did not cross zero appear in bold. The significance of each variable was assessed using chi-square tests (Chisq), while the significance of each level of a categorical variable was evaluated against a reference level (noted ‘Ref’) according to whether their confidence intervals (CI) overlap or not.

Response variable: Aggression during a month of the mating season					
Fixed Factor	Level	Estimate	CI 95%	Chisq	P-value
Male Rank	Alpha (Ref: Non-alpha)	0.610	[0.050;1.171]	4.552	0.033
Male age		0.050	[-0.067;0.167]	0.707	0.400
Operational Sex Ratio		0.315	[-0.005;0.634]	3.728	0.054

2.4 Discussion

We found support for all three core predictions of the sexual coercion hypothesis in mandrills. First, swollen females received significantly more male aggression than other females. Elevated aggression towards females around ovulation has been observed frequently in mammals, even in species where females dominate males socially (e.g. spotted hyena (*Crocuta crocuta*): Szykman et al., 2003), suggesting that sexual coercion is widespread. Second, swollen female mandrills were significantly more injured than females in other reproductive states. Such injuries are most likely caused by males because aggression from other groupmates did not intensify during female sexual receptivity. Male aggression thus potentially causes important fitness costs in female mandrills, as shown in other mammals exhibiting sexual coercion (e.g. feral sheep (*Ovis aries*): Réale, Boussès, and Chapuis, 1996; bottlenose dolphins (): Wallen et al., 2016; chacma baboons: Baniel, Cowlshaw, and Huchard, 2017; chimpanzees: Watts, 2022). These fitness costs may push females to comply and copulate more with aggressive males to avoid conflict escalation and the associated risk of injury (Cassini, 2020; Baniel et al., 2021). Third, our analysis suggests that increased and repeated male aggression before the receptive period increases male mating success with the targeted female at times where she is most likely fertile. This correlation holds true both with severe aggression and non-physical threats, which are only moderately correlated. Most studies on sexual coercion have fo-

cused exclusively on severe aggression (Baniel, Cowlshaw, and Huchard, 2017; Muller et al., 2007) but our results indicate that male mandrills use a wide aggressive repertoire, including threats, to coerce females. Male threats (such as head-bob or ground-slap) typically produce little immediate behavioural reactions in females, but could increase their sexual compliance with the aggressor when exerted repeatedly (Swedell and Schreier, 2009), especially when male-female power asymmetry is high, as in mandrills, which display one of the largest sexual dimorphism in primates.

The observed correlation between male aggression and mating success does not seem well-explained by alternative interpretations to sexual coercion, as we did not find evidence supporting a female preference for particularly aggressive males. Females could potentially use male aggression as a badge of status (Muller et al., 2007; Setchell and Jean Wickings, 2005) to infer male competitive abilities, which may provide females with direct or indirect benefits (Cordero and Eberhard, 2003; Pizzari and Snook, 2003). However, in our data, variation in aggression rates among heterosexual dyads explain male mating success better than male general aggressiveness, suggesting that male mating success reflects relational properties more than male aggressive phenotype. It is further possible that male-female aggression rates directly reflect differences in male-female spatial proximity, where males would direct more aggression to females who would happen to stand around them. However, patterns of spatial ranging in social groups are far from random, and typically reflect the group social structure, in the form of differentiated relationships (e.g. spatial proximity is positively correlated to the strength of social bond in wild boars (*Sus scrofa*); Podgórski et al., 2014). In such context, male-female aggressive rates are more likely to reflect the existence of such differentiated social bonds between males and females than a scenario where a male would attack females who randomly happen to stand in their proximity. In line with this, recent studies in chimpanzees indicate that males preferably coerce their affiliated female partners (Reddy and Mitani, 2020), mirroring observations in humans where intimate partner violence is extensive (Basile, 2002).

Our analyses reveal important aspects of the ecology of sexual coercion in mandrill societies. While we did not find evidence for sexual harassment, our results suggest that repeated aggression over extended periods increases mating probability to aggressors once

females become fertile, and may further encourage them to stay around males who mate-guard them, as observed in hamadryas baboons (*Papio hamadryas*; Swedell and Schreier, 2009). Sexual intimidation has previously been shown in chimpanzees and chacma baboons (Muller et al., 2007; Baniel, Cowlshaw, and Huchard, 2017), two species characterized by relatively high male violence towards females. We found that male mandrills use severe aggression towards swollen females more often on average than chacma baboons (mean \pm SD: 0.350 \pm 0.950 vs 0.130 \pm 0.190 times per hr; Baniel, Cowlshaw, and Huchard, 2017) and at a rate that lies high within the chimpanzee's reported range (Muller et al., 2007; Watts, 2022). Such frequent use of coercion by mandrill males may relate to the fact that - unlike chimpanzees and chacma baboons - they breed seasonally, thus have a limited time window to achieve mating. Yet, swollen female mandrills are injured ca. three times less on average than chacma baboons (mean \pm SD: 0.005 \pm 0.016 vs 0.014 \pm 0.022 injuries per day; Baniel, Cowlshaw, and Huchard, 2017). Hence, although male to female aggression is more frequent in mandrills than in chacma baboons, violent aggression resulting in serious injuries is probably less common.

Moreover, the fact that we did not find any evidence of punishment, likely reflects the absence of exclusive mating bonds in mandrills (outside mate-guarding episodes) and the ability of females to sneakily escape male monopolization strategies in their dense habitat. Punishment by males in response to female sexual activity with a rival has, for instance, been reported in geladas (*Theropithecus gelada*) which live in more open habitat (le Roux et al., 2013) and where one leader male can aggressively defend sexual access to females from his family unit (Snyder-Mackler, Alberts, and Bergman, 2012). To sum-up, our results are generally consistent with expectations based on the socioecology of mandrills, who (i) are highly dimorphic thus where males pay low costs of intersexual aggression, (ii) breed seasonally, and where males face high pressure to mate in a relatively short period, and (iii) live in a polygynandrous mating system, and where males and females form differentiated social bonds - allowing intimidation to function - but no exclusive mating bonds, preventing the use of punishment by males.

Male dominance status appeared influential in their coercive tendencies. Alpha male mandrills were more aggressive towards females during the mating season, and they copulated significantly more with females than non-alpha males. Given the high repro-

ductive skew in favour of alpha male mandrills (Charpentier et al., 2020; Charpentier et al., 2005), this result suggests that sexual coercion is an effective male reproductive strategy, although more detailed analysis is necessary in order to confirm the relationship between male coercion and reproductive success. Dominant males in other primates similarly use long-term coercive strategies to constrain female promiscuity and impose closer proximity (e.g. hamadryas baboons: Swedell and Schreier, 2009). However, in other species, such as orangutans, subordinate males have been reported to be more coercive, and use forced copulation more often than dominant males (Kunz et al., 2021b). The use of coercive strategies may be rendered more difficult for subordinate males in group-living species compared to solitary ones, such as orangutans, if other group members, including the alpha male, occasionally step in to defend the victim.

Our analyses further highlight that all females are not equally targeted by males. High-ranking females specifically receive more male aggression than low-ranking females, which may reflect male mating preferences because dominant females show better reproductive performances than subordinates (Setchell et al., 2002; Dezeure, Charpentier, and Huchard, 2022). Similarly, male hyenas mate preferentially with high-ranking females (Szykman et al., 2001; Keddy-Hector, 1992) while male chimpanzees direct more aggression towards parous than nulliparous females (Muller et al., 2007) and prefer old females (Muller, Thompson, and Wrangham, 2006), who have a higher rank and reproductive success than younger ones (Pusey, Williams, and Goodall, 1997). This result indicates that the highest costs of coercion are born by the most attractive females, as found in chimpanzees (Muller et al., 2007).

An important question remains whether and how female mandrills may navigate such a coercive landscape while still possibly expressing some mate choice (Setchell, 2016). Chimpanzee studies have raised contrasting results, with sexual coercion in some populations (Muller et al., 2007; Watts, 2022) versus female mate choice in other populations (Stumpf and Boesch, 2006; Kaburu and Newton-Fisher, 2015). It is possible that such conflicting results reflect differences across populations, or alternatively methodological differences between studies, where studies of mate choice often measure female choice through differential rates of approaches of males by females (Stumpf and Boesch, 2006), while studies of sexual coercion correlate aggression and mating rates (Muller et al., 2007;

Baniel, Cowlshaw, and Huchard, 2017). The growing body of work on sexual coercion generally casts doubts on inferring mate choice from rates of approaches (Muller et al., 2011), as such approaches, as well as any affiliative interaction, could instead reflect female attempts to appease coercive males (Baniel et al., 2021). Alternatively, it's possible that sexual coercion can co-occur with female mate choice, as is the case in humans.

Our work underlines the existence of sexual coercion in mandrills while evidence for female choice remains scarce in this species (Setchell, 2016). It is therefore hard, at this stage, to evaluate the freedom left for females to express their own reproductive strategies. Nevertheless, several mechanisms may help females to mitigate the constraints set by male coercion. They may form alliances with other females to defend themselves (Clutton-Brock and Parker, 1995b; Paoli, 2009) or heterosexual bonds with males who protect them (Smuts, 1995). They may also appease male aggressors to limit the risk of escalation and injuries (Swedell and Schreier, 2009; Baniel et al., 2021), fight-back against aggressors, flee, hide or close their genitals (Eberle and Kappeler, 2004; Huchard et al., 2012). Female mandrills may use some of these strategies, as their behavioural repertoire includes avoiding male approaches, laying down when males attempt to copulate with them, refusing some mating attempts (Setchell, 2016; Setchell, 2005), interrupting copulation by fleeing away, seeking support from subordinate males against dominant ones (MJEC personal observation) or even forming violent coalitions against high-ranking males (Setchell, Knapp, and Wickings, 2006; NS personal observation). In addition, previous studies on primates have demonstrated that female reproductive synchrony and large group sizes limit female monopolisation by males (across species: Ostner, Nunn, and Schülke, 2008; in mandrills: Charpentier et al., 2005) and increase the potential for females to express their strategies, including mate choice or promiscuity (Ims, 1990; Fürtbauer et al., 2011). Therefore, the extreme size of mandrill social groups along with female reproductive synchrony, may facilitate the expression of female reproductive strategies and reduce male coercion.

Here we report new evidence for sexual intimidation in a species where males, despite being much larger than females, are not conspicuously aggressive towards them (at least from a human observer perspective). The temporal uncoupling between male aggression and copulation explains why sexual intimidation may have long been overlooked, while

it increasingly appears influential at shaping the social structure and mating system of polygynandrous mammals (Clutton-Brock, 2021).

2.5 Supplementary material

Sexual harassment and sexual punishment

To study sexual harassment and sexual punishment we used only 5 minutes-long (complete) focal observations performed on adult swollen females or adult males. To test for sexual harassment, we assessed whether a male directed aggression towards a swollen female during the first half of the focal observation (150 seconds). If aggression occurred ('post-aggression observation'; Figure S2a, middle line), we assessed whether a copulation occurred between the female and the male within a 150 second-time window following this aggression. We planned to use a post-conflict matched-control statistical framework to test whether females were more likely to copulate with a male immediately after he attacked her versus in absence of aggression from him. In short, we had planned to match each post-aggression observation with matched-control observations (i.e., observations of the same individuals in which no male aggression occurred during the first half; Figure S2a) and compare the likelihood of copulation in those two different contexts. The time span of 150 seconds was chosen as the maximum length allowing post-aggression and matched-control observation to be of equal length. Similarly, to test for sexual punishment we assessed whether a male copulated with a swollen female during the first half of the focal observation. If a copulation occurred ('post-copulation observation'; Figure S2b, middle line), we assessed whether an aggression from another male towards the copulating female was observed within a 150 second-time window following the copulation. We had planned to use a similar post-copulation matched-control analysis to test whether females were more likely to be attacked in the post-copulation observations versus in the matched-control observations without copulation. However, since we found few or no instance(s) of post-conflict copulations and post-copulation aggression, we did not pursue those analyses and only report raw data.

Testing the “aggressive male phenotype” hypothesis

We explored an alternative scenario to sexual coercion, the “aggressive male phenotype” hypothesis, by testing whether males that are more aggressive towards any groupmate

are also those that copulate the most because aggression may act as a sexual trait chosen by females. We reran the same GLMM as the one used for testing the occurrence of intimidation, including as an explanatory variable, in addition to the aggression towards the given female, the rate of the overall aggression the male directed towards all groupmates except adult females during the corresponding mating season. Such overall aggression was quantified as the number of aggression events initiated by a given male towards any non-adult female group member divided by the total time of observation of this male during a given mating season.

The overall aggression displayed by males towards non-adult females did not influence their copulation success with adult females suggesting that females do not copulate more with the most aggressive males of the group, but with males that have been the most aggressive to them before their fertile (swollen) period. In particular, in the model including both aggression rates (overall and dyadic), the aggression rate towards all groupmates except adult females was not significant ($\text{Chisq}=2.12$, $p\text{-value}=0.15$) but the rate of aggression towards the dyad female was marginally significant ($\text{Estimate}=1.529$, $\text{CI95\%}=[-0.039;3.097]$, $\text{Chisq}=3.654$, $p\text{-value}=0.056$) in comparison to the model without the overall aggression rate where the dyadic aggression rate was clearly significant (Table 3).



Figure S1: Analytical design for the tests of sexual intimidation. The swollen period is shown in blue, and the “aggression windows” are depicted in red. The top line represents the original test of intimidation. The bottom line represents the test with the alternative “aggression window”. On the horizontal axis, the relevant temporally consecutive events (from left to right) are depicted (the distances among them can contextually fluctuate considerably). “Onset of mating season”: onset of mating season (for residents) or arrival in the group (for non-residents), “Swelling”: onset of the swollen period of the female, “Max”: onset of the maximal swollen period of the female, “Max end”: end of the swollen period (the last day of maximal swelling) and “End”: complete deflation of the sexual swelling that started in “MaxEnd”.

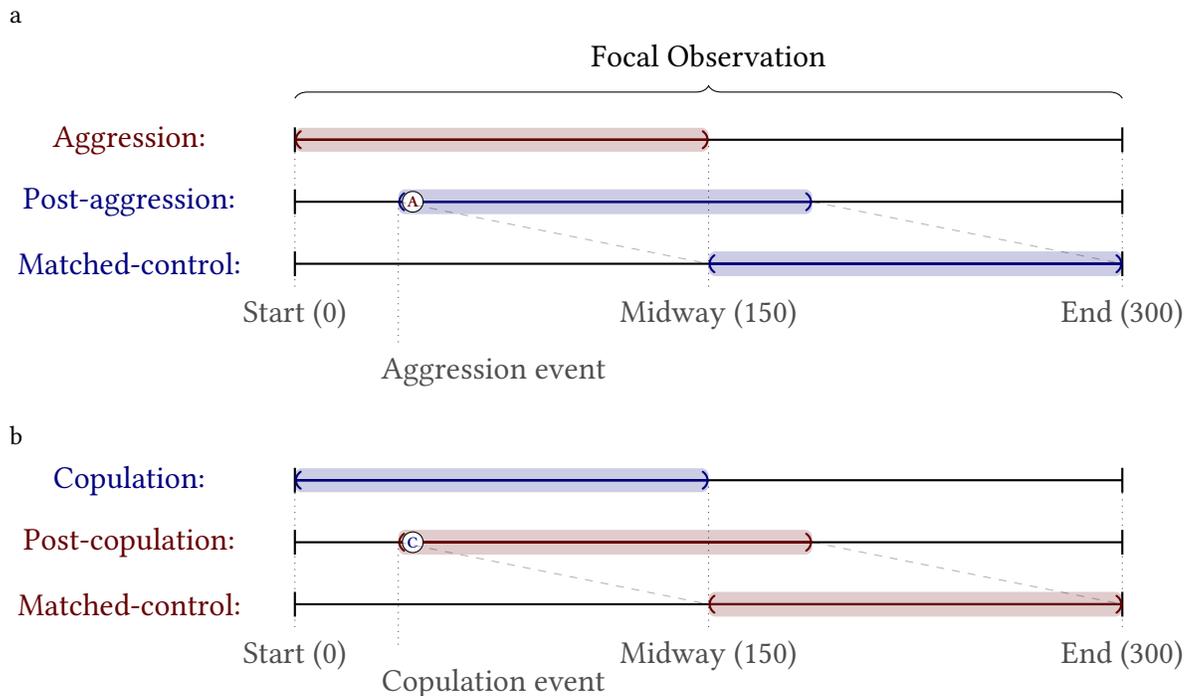


Figure S2: Analytical design for the planned test of sexual harassment and sexual punishment. (a) For each female or male focal observation, if an aggression occurred from a male towards a swollen female in the first 150 seconds (red), we assessed whether copulation of the same heterosexual dyad occurred within the 150 seconds following the aggression (post-aggression observation, blue – middle line); for the matched-control observations where no aggression occurred in this dyad in the first 150 seconds of the focal, we assessed whether a copulation was observed within the dyad during the last 150 seconds of the focal observation (blue – bottom line). (b) For each female or male focal observation, if a copulation occurred between a male and a swollen female in the first 150 seconds (blue), we examined whether aggression from another male towards the copulating female occurred within the 150 seconds following the copulation (post-copulation observation, red – middle line); for the matched-control observations where no copulation occurred in this dyad in the first 150 seconds of the focal, we assessed whether an aggression was observed during the last 150 seconds of the focal observation (red – bottom line).

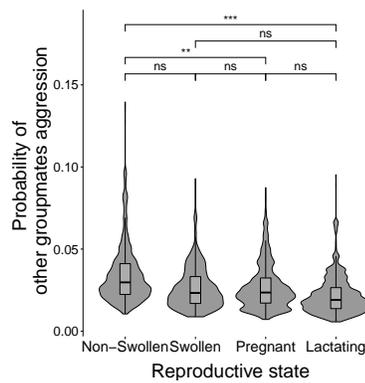


Figure S3: Predicted probability of aggression received by adult females from groupmates other than adult males in relation to female reproductive state. The fitted values of the GLMMs are shown on the Y-axis. The violin plots show the probability density. Pairwise comparisons across female reproductive states and corresponding p-values are shown. ‘ns’, not significant: $p > 0.05$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

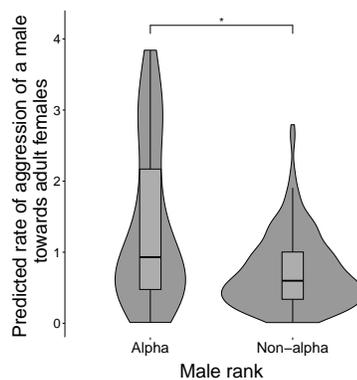


Figure S4: Predicted aggression rate of males towards adult females in relation to male rank (alpha vs non-alpha). The fitted values of the GLMM are shown on the Y-axis. The violin plots show the probability density. Pairwise comparisons across female reproductive states and corresponding p-values are shown. ‘ns’, not significant: $p > 0.05$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

Table S1: Summary of predictions and analyses with relevant sample size, figures and tables. All models followed a binomial distribution. S: swollen, NS: non-swollen, P: pregnant, L: lactating.

Prediction	Resp. Variable	Sample	Fixed factors	Random Factors	Tabs & Figs
Swollen females receive more male aggression (1st prediction)	Probability of receiving male aggression during a focal observation	31633 focals (2113h) on 80 females	Reproductive state (NS, S, P, L) Female rank Female parity Group sex ratio	Female identity Year of observation	Figure 1a Table 1
Swollen females do not receive more aggression from other groupmates	Probability of receiving other groupmate aggression during a focal observation	31633 focals (2113h) on 80 females	Reproductive state (NS, S, P, L) Female rank Female parity Group sex ratio	Female identity Year of observation	Figure S4 Table S2
Swollen females are at higher risk of injury (2nd prediction)	Probability of having an injury	116.291 female.days (79 females and 2712 days)	Reproductive state (NS, S, P, L) Female rank Female parity Group sex ratio	Female identity Year of observation	Figure 1b Table 2
Male aggression increases male mating success (3rd prediction) & Aggressive phenotype hypothesis	Probability of copulation during the relevant period	Harassment/Punishment: 1023 focals (85h) on 55 swollen females & 3590 focals (299h) on 34 males Intimidation: 16212 focals (1116h) on 79 females & 5178 focals (366h) on 33 males	Male aggression (during the relevant period, towards the relevant individuals) Female rank Female parity Operational sex ratio Male rank (in interaction with aggression)	Female identity Male identity Year of observation	Figure 1c Figure S1 Figure S2 Table 3 Table S3 Table S4
Alpha males are more aggressive towards females	Aggression towards adult females	16212 focals (1116h) on 79 females & 5178 focals (366h) on 33 males	Male rank Male age Operational sex ratio	Male identity Year of observation	Figure S4 Table S4

Table S2: Aggression from other groupmates and female reproductive state. Significant p-values and confidence intervals (CI) that did not cross zero appear in bold. The significance of each variable was assessed using chi-square tests (Chisq), while the significance of each level of a categorical variable was evaluated against a reference level (noted 'Ref') according to whether their confidence intervals overlap or not.

Response variable: Probability of receiving aggression from other groupmates (0/1)					
Fixed Factor	Level	Estimate	CI 95%	Chisq	P-value
Reproductive State	Swollen (Ref: Non-Swollen)	-0.192	[-0.474;0.090]	21.386	< 0.001
	Pregnant (Ref: Non-Swollen)	-0.241	[-0.412;-0.070]		
	Lactating (Ref: Non-Swollen)	-0.432	[-0.618;-0.246]		
	Swollen (Ref: Lactating)	0.239	[-0.056;0.534]		
	Pregnant (Ref: Lactating)	0.191	[0.003;0.379]		
	Swollen (Ref: Pregnant)	0.049	[-0.234;0.331]		
Female Rank	Medium Rank (Ref: High Rank)	0.256	[-0.090;0.602]	17.765	< 0.001
	Low Rank (Ref: High Rank)	0.578	[0.308;0.847]		
Female Parity	Parous (Ref: Nulliparous)	-0.352	[-0.683;-0.021]	4.347	0.037
Group Sex Ratio		-0.024	[-0.062;0.014]	1.533	0.216
Observation time		0.028	[-0.041;0.098]	0.647	0.421

Table S3: Male aggression and mating success (intimidation; alternative “aggression window”). (a) Probability of copulation of a male-female dyad during female’s swollen period in relation to the rate of aggression received from the male during the female’s swollen period. Probability of copulation of a male-female dyad during female’s swollen period in relation to the rate of (b) severe aggression or (c) threats received from the male before the female’s swollen period. Significant p-values and confidence intervals (CI) that did not cross zero appear in bold. The significance of each variable was assessed using chi-square tests (Chisq), while the significance of each level of a categorical variable was evaluated against a reference level (noted ‘Ref’) according to whether their confidence intervals overlap or not.

Response variable: Mating during the swollen period (0/1)						
Test	Fixed Factor	Level	Estimate	CI 95%	Chisq	P-value
a. Aggression in swollen period	Aggression Rate		0.173	[-1.016;1.363]	0.082	0.775
	Male Rank	Alpha (Ref: Non-alpha)	1.261	[0.542;1.979]	11.819	0.001
	Female Rank	Low Rank (Ref: High Rank)	0.617	[-0.233;1.467]	2.030	0.362
		Medium Rank (Ref: High Rank)	0.288	[-0.985;1.560]		
	Female Parity	Parous (Ref: Nulliparous)	0.304	[-1.675;2.282]	0.090	0.764
	Operational Sex Ratio		0.112	[-0.373;0.597]	0.205	0.65
	Observation Time		0.461	[0.160;0.761]	9.030	0.003
b. Severe aggression only	Aggression Rate		6.307	[0.927;11.686]	5.280	0.022
	Male Rank	Alpha (Ref: Non-alpha)	1.291	[0.531;2.050]	11.086	0.001
	Female Rank	Low Rank (Ref: High Rank)	0.737	[-0.153;1.627]	2.879	0.237
		Medium Rank (Ref: High Rank)	0.724	[-0.639;2.087]		
	Female Parity	Parous (Ref: Nulliparous)	-0.456	[-2.843;1.931]	0.140	0.708
	Operational Sex Ratio		0.036	[-0.494;0.565]	0.017	0.895
	Observation Time		0.537	[0.211;0.863]	10.446	0.001
c. Threats only	Aggression Rate		2.111	[-0.465;4.688]	2.580	0.108
	Male Rank	Alpha (Ref: Non-alpha)	1.247	[0.511;1.983]	11.026	0.001
	Female Rank	Low Rank (Ref: High Rank)	0.682	[-0.182;1.545]	2.609	0.271
		Medium Rank (Ref: High Rank)	0.673	[-0.672;2.019]		
	Female Parity	Parous (Ref: Nulliparous)	-0.510	[-2.854;1.834]	0.182	0.67
	Operational Sex Ratio		0.005	[-0.509;0.519]	0.000	0.985
	Observation Time		0.544	[0.220;0.868]	10.817	0.001

Competing interests: The authors declare no competing interests.

Ethics: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This study was approved by the CENAREST institute (permit number, AR003/20/MESRSTT/ CENAREST/CG/CST/CSAR) and adhered to the legal requirements of Gabon for the ethical treatment of non-human primates.

Data accessibility: The datasets and scripts necessary to replicate analyses included in this article are deposited in the public depository: <https://doi.org/10.5281/zenodo.6607803>

Authors' contributions: N.S., M.J.E.C., and E.H. designed the study; B.R.T. and P.A.R collected behavioural data; N.S. performed the statistical analyses; N.S., M.J.E.C., E.H. wrote the original draft and all authors critically contributed to the draft and approved submission.

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Chapter 3

Socially bonded female mandrills face more sexual coercion

Authors

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Abstract

Increasing evidence suggests that sexual coercion is a widespread form of sexual conflict that increases male mating success and inflicts costs to females. Although variation in male coercive tendencies starts to be investigated, little is known about the traits and strategies that may mitigate females' exposure to coercion. Here we investigate the sources of between-female variation in exposure to coercion in a natural mandrill (*Mandrills sphinx*) population. We specifically ask if socially bonded females, who usually enjoy higher fitness and more social support, may face less sexual coercion. In contrast to our predictions, we found that females receive most coercion from those males with whom they form stronger affiliation bonds. Second, females who maintain bonds with more males, or a stronger bond to one particular male, receive more coercion across all males. Third, greater integration in the female social networks also promotes the exposure of females to coercion. Finally, we tested if this positive effect of social integration on coercion may be indirectly mediated by female attractiveness (indexed by their reproductive success) and/or retaliation potential (indexed by their rank in the intersexual hierarchy), in case male aggression escalates towards more attractive or resistant females. Our results instead indicate a direct effect, possibly reflecting a greater 'public exposure' of females that are central in the social networks. This study shows that neither intersexual nor intrasexual bonds can be protective against sexual coercion faced by female mandrills, and instead identifies a hidden cost of their social connections, which translate into a greater exposure to coercion.

3.1 Introduction

The control over reproductive opportunities is a fundamental aspect of animal social evolution (Clutton-Brock, 2021) that often leads to competition within (Clutton-Brock and Huchard, 2013b) and between the sexes (Davidian et al., 2022; sexual conflict: Parker, 1979). In species characterized by sexual conflict over reproductive control, males often aim to maximize reproductive opportunities by monopolizing females sexually, while strategies evolve in females to minimize such male control (Parker, 2006). Sexual co-

ercion is an obvious form of sexual conflict that includes strategies such as forced copulation, sexual harassment, intimidation, infanticide, coercive mate-guarding or post-copulation punishment. It is increasingly recognized as a prominent male behavioural toolkit improving male mating success and inflicting costs to females (Smuts and Smuts, 1993; Clutton-Brock and Parker, 1995b) in the form of injuries (Baniel, Cowlshaw, and Huchard, 2017), stress (Muller et al., 2007) or by heavily constraining their reproductive strategies. Although some studies have focused on the male perspective, investigating the benefits of coercion (Feldblum et al., 2014), or variation among males in coercive tendencies (Reddy et al., 2021), much less is known about the female perspective, and specifically how females may minimize the amount of coercion they receive or balance its costs.

Female strategies to retain or re-gain reproductive control are manifold (Davidian et al., 2022). They may include female physiological adaptations to minimize male monopolization potential, such as fertility synchrony (Ostner, Nunn, and Schülke, 2008) and unreliable fertility signals (Douglas et al., 2016) or concealed ovulation (Schoröder, 1993; Heistermann et al., 2001) to deceive males. To counter male monopolization attempts, females may also use behavioural strategies, such as sneaky copulations (le Roux et al., 2013) and in social species, particularly, they may also use social relationships to prevent or resist male coercive tactics. For example, female pinnipeds may breed in large groups to dilute the risk of male harassment (Cappozzo, Túnez, and Cassini, 2008) while female primates may form long-term associations with particular males to minimize the risk of conspecific aggression (Nguyen et al., 2009) and particularly infanticide (Van Schaik and Kappeler, 1997; Palombit, 1999).

A large body of work has documented important fitness benefits associated to social bonds and social integration, across a variety of species (recently reviewed by Snyder-Mackler et al., 2020). The mechanisms mediating these effects remain partially understood, and may include reduced stress levels in individuals that maintain numerous or strong social connections (Seeman et al., 2002), as well as a decrease or protective effect against conspecific harassment. For example, heterosexual bonds are associated with a reduced risk of mortality in humans (Waldron, Hughes, and Brooks, 1996; Gardner and Oswald, 2004; Holt-Lunstad, Smith, and Layton, 2010; Staehelin et al., 2012), of conspe-

cific harassment and mortality in baboons (Lemasson, Palombit, and Jubin, 2008; Archie et al., 2014) and of infanticide in several primate species (Palombit, 1999). In addition female Assamese macaques (*Macaca assamensis*) that form stronger affiliation bonds with certain males, receive less aggression from these males (Haunhorst et al., 2017), presumably because males don't need to coerce their female partners to mate with them. Moreover, female-female affiliation bonds might also prove protective when potential aggressors may hesitate to assault socially-bonded females that may form coalitions to retaliate against them Bro-Jørgensen, 2011; Smuts and Smuts, 1993. For example, female feral horses which are more socially integrated with other females receive less male harassment (Cameron, Setsaas, and Linklater, 2009). Female-female coalitions occur in different taxa, especially where females are philopatric and get support from their maternal kin during conflicts (Holekamp and Smale, 1991) as in chacma baboons (*Papio ursinus*; Silk et al., 2010a) and spotted hyenas (*Crocuta crocuta*; Vullioud et al., 2019). Overall, the fitness benefits of heterosexual and intrasexual bonds that have been documented in multiple taxa (Snyder-Mackler et al., 2020) may be partially mediated by the protection they offer against harassment by conspecifics, including sexually coercive males ('protective bonds hypothesis').

Nonetheless, the protective potential of social bonds against male coercion may be counterbalanced by additional, opposite selective pressures that make bonds costly rather than protective ('costly bonds hypothesis'). First, males commonly prefer to mate with females who have a history of successful reproduction, and may thus be more coercive with them ('attractiveness hypothesis'). For example, male chimpanzees (*Pan troglodytes*) mate preferentially with older females (Muller, Thompson, and Wrangham, 2006) who have higher reproductive success (Pusey, Williams, and Goodall, 1997) and they are also more coercive with them than with younger females (Muller et al., 2007). Therefore, more bonded females, which often have higher reproductive success (wire-tailed manakins (*Pipra filicauda*): Ryder et al., 2009; mandrills: Charpentier et al., 2012), may receive more male coercion because coercive males prefer them as mates. Second, in agonistic interactions, which are often terminated by the submission of the subordinate individual without escalation (Drews, 1993), the risk of retaliation might be greater when power asymmetries between the competing individuals are low, because they have similar physical strength or dominance rank (Clutton-Brock et al., 1979; Gordon and Lea, 2016); accordingly, more

powerful women may respond to male sexual harassment more assertively (Gruber and Bjorn, 1986; Folke et al., 2020). Those females who are more bonded may enjoy higher social support and dominance rank (ravens (*Corvus corax*): Braun and Bugnyar, 2012; mandrills: Smit, Huchard, and Charpentier, 2022), and may therefore receive more male coercion if they retaliate more in response to male aggression ('retaliation hypothesis'). Finally, more bonded females which may occupy central positions in a group and typically interact more with their groupmates than peripheral females may also be more exposed to coercive males, and thus receive more coercion across all males ('public exposure hypothesis').

Here we study the influence of inter- and intrasexual social bonds on the intensity of coercion that females receive from males, using a 9-year dataset on wild mandrills. Mandrills are members of the *Cercopithecidae* family that live in polygynandrous groups and breed seasonally (Dezeure, Charpentier, and Huchard, 2022). Males use sexual intimidation (Smit et al., 2022), a form of sexual coercion which increases their future (rather than immediate) mating probability with their victims (Smuts and Smuts, 1993), and mate-guard females when they display maximal sexual swellings around ovulation (Setchell, Charpentier, and Wickings, 2005a). Female mandrills are philopatric and form strong social bonds with groupmates showing biases in favour of close maternal and paternal kin (Charpentier et al., 2020). In contrast, most males enter the group at the onset of the mating season and only a few remain in the group during the next birth season (Brockmeyer et al., 2015). This temporal residency of males in the group suggests that males are likely less socially integrated than females. More socially integrated females exhibit younger age at first reproduction than less socially integrated females (Charpentier et al., 2012), while both male and female mandrills that are more socially integrated within the female affiliation social network dominate more groupmates of either sex (Smit, Huchard, and Charpentier, 2022). Mandrills exhibit an extreme sexual size dimorphism (Setchell et al., 2001), and females, which are ~3-times lighter than males, may not be able to confront them alone. Nonetheless, females can form exceptionally violent coalitions against males (Setchell, Knapp, and Wickings, 2006).

We test the 'protective (HP1) versus costly bonds hypothesis' (HP2) through three main predictions. First, we predict that female mandrills who form affiliation bonds with males

receive less (Prediction 1.1) vs more (P2.1) coercion from them. Second, we predict that females with stronger bonds with a certain male ('top male partner') receive less (P1.2) vs more (P2.2) male coercion from all other males (compared to females with weaker bonds with their top male partner); and females with stronger bonds with all males receive less (P1.3) vs more (P2.3) coercion from their 'top male coercer' (compared to females with weaker bonds with all males). Third, we predict that a female's position in the female social network and/or her number of maternal kin present in the group protects her from (P1.4) vs exposes her to (P2.4), male coercion. In a second part, and based on the result that more integrated females in the female social network receive more male coercion in support of prediction P2.4 generated by the 'costly bonds hypothesis', we further investigate two indirect (P2.4a & b) and one direct (P2.4c) pathway for such relationship (Figure 1). We investigate, namely, whether well-connected females receive more aggression because they are attractive due to their higher reproductive success ('attractiveness hypothesis', P2.4a), because their social support makes them more powerful thus more likely to retaliate ('retaliation hypothesis', P2.4b) or simply because their central position makes them more exposed to male coercion ('public exposure hypothesis', P2.4c). In the first case, because male mandrills are not permanent residents, they may be unable to know a female's past reproductive history and thus, they may infer it from females' social environment, targeting females who are surrounded by more partners and offspring. In the second case, we approximate female intersexual power by her dominance rank in the intersexual hierarchy.

3.2 Methods

Study population

We studied a natural population of mandrills living in Southern Gabon, in a private park (Lékédi Park), established after two releases of captive individuals from CIRMF (Centre International de Recherches Médicales de Franceville, Gabon) in 2002 and 2006 (Peignot et al., 2008). The study group is habituated to human presence thanks to the set-up of a long-term field project in 2012 that aims to study the life-history, ecology and behaviour

of these mandrills. In late 2021, the group consisted of c.a. 220 individuals including only 7 females that were born in captivity, all other individuals being born in the wild (for more details on the origins of the group see (Brockmeyer et al., 2015)). We used data collected for 9 consecutive years (2012 to 2021, excluding 2020 due to COVID19 pandemic-related disruptions) on a total of 51 adult females aged 4 yrs and older and 39 subadult and adult males aged 9 yrs and older. We considered the mating season to occur from April 1st to September 30th (Dezeure, Charpentier, and Huchard, 2022).

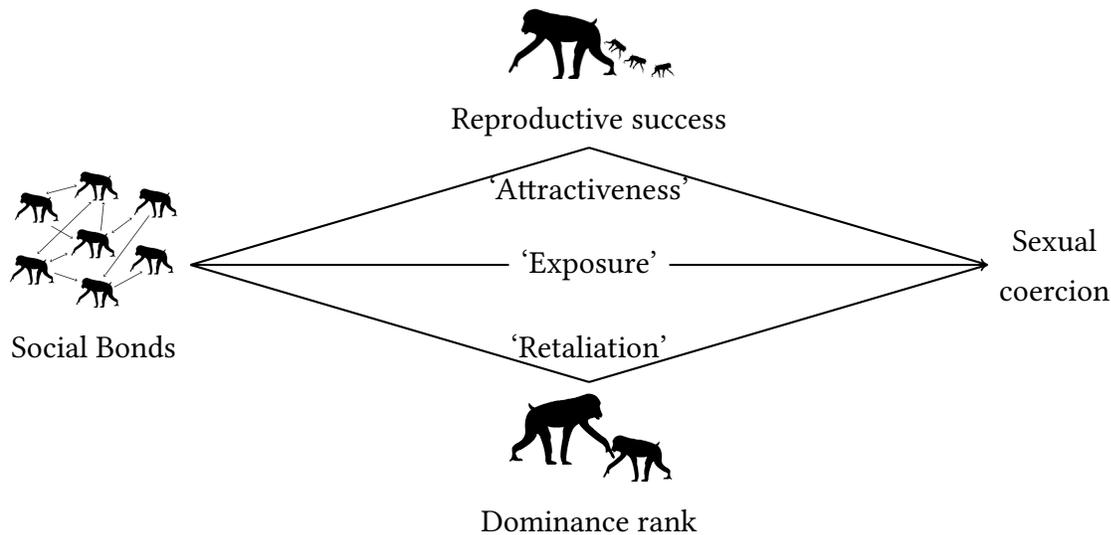


Figure 3.1: The direct and indirect effects of female social bonds on the coercion a female receives from all males. The different effects, based on the working hypotheses, are represented by three pathways: indirect effect of social bonds on sexual coercion mediated by female reproductive success ('attractiveness hypothesis'; top), direct effect ('public exposure hypothesis'; middle), and indirect effect mediated by female dominance rank ('retaliation hypothesis'; bottom).

Behavioral observations

Observers blind to the topic of this study conducted daily *ad libitum* behavioural observations and 5-min focal sampling on individually-recognized male and female mandrills. We considered a total of 24169 focal observations (18767 observations totalizing 1300 hours on females and 5402 observations equating to 383 hours on males). During focal observations, agonistic (aggressive: grasping/hitting, biting, chasing, lunging, slapping

the ground and head bobbing; submissive: avoidance, displacement, escape and submissive vocalization) and grooming interactions were recorded along with other behaviours. These observations were interspersed with up to three proximity scans (every 2 minutes) recording the identities of all individuals located within five meters from the focal individual. Data on the life-history of the studied mandrills were also available.

Individual traits

Dominance ranks

We used the function *DS* from the R package *EloRating* (Neumann et al., 2011) to compute intersexual hierarchies based on submissive dyadic interactions that were recorded between males and females during focal or *ad libitum* observations, as per (Smit, Huchard, and Charpentier, 2022). This function produces individual David's scores (David, 1987) using the number of agonistic interactions that an individual wins/loses. Differences between individual scores measure dominance asymmetries, which we calculated for each male-female dyad. Previous results have shown that high-ranking female mandrills receive significantly more male aggression than low-ranking ones (Smit et al., 2022) and high-ranking males are more coercive than low-ranking ones. In our models described below, therefore, we used both female and male rank as control variables.

Age

The exact birth date was known for 21 of the studied individuals. For the remaining 69 individuals, we estimated age based on body condition and patterns of tooth wear and eruption (Galbany et al., 2014). For 37 individuals the error of the estimation was maximum 1 year and for 32 individuals it was between 1 and 3 years. Previous results showed that female mandrills outrank adult male mandrills that are either relatively young or old, but usually not when they are in their prime (Setchell, Wickings, and Knapp, 2006). We therefore considered male age (and its quadratic term) in our models below to control for the fact that males in their prime may be more coercive towards females than young or old males. In addition, we consider female age (and its quadratic term) to control for the

fact that mid-aged females may receive more male coercion, because they are more attractive due to their higher reproductive success documented in other mammals (Alpine ibex (*Capra ibex*): Rughetti et al., 2015; chimpanzees: Sugiyama, 1994), than young or old females.

Reproductive state

Observers recorded the reproductive state of each female mandrill aged 3 yrs and older on a near-daily basis. During oestrous periods, which usually occur during the mating season, females exhibit sexual swellings which gradually inflate (recorded on a scale from 0 to 3 by increments of 0.5; Dezeure, Charpentier, and Huchard, 2022) until reaching a maximal size, around ovulation, before deflating. Here we considered only conception cycles (i.e., which resulted in a birth) and calculated male aggression from the beginning of the mating season until this conception cycle in order to include the cycling period – and all swollen episode - in case a female cycled more than once within a mating season.

Reproductive success

We calculated the number of surviving offspring (surviving >6 months) for each female and each mating season, as a proxy of female reproductive success.

Matriline size

For each female, matriline size was calculated as the number of adult females with whom she was sharing a common mother or maternal grand-mother which were present in the group at the start of each mating season. Maternally related females who were released in two different bouts from CIRMF (in 2002 vs in 2006) were considered as belonging to two distinct matrilines due to major social disruptions affecting the female social structure following their re-introduction. In particular, all females released in 2006 ended-up in a lower rank position (MJEC unpublished data).

Sex ratio

Monthly operational sex ratios (OSR) were calculated as the number of adult females that conceived that month divided by the number of subadult and adult males (i.e., aged ≥ 9 years) that were censused in the group at least two days that month. For each mating season, we averaged monthly OSRs across the six months of the season. We used OSR in our analysis to control for the fact that male-biased OSR may be associated with increased coercion due to higher male-male competition.

Quantifying sexual coercion

For each female-male dyad and each mating season, we indexed sexual coercion as the number of male aggressive events towards the female starting at the male's arrival in the group that year (for immigrant males) or at the arrival of the first immigrant male in the group that year (for resident males) and ending on the first day of the female's conception oestrous cycle, i.e. the first day she was sexually swollen (Smit et al., 2022). In a given mating season, we considered as residents those males who were censused in the group in the three months preceding the mating season (January-March), and as immigrants those who were first censused during the mating season (April-September). In addition, and for each oestrous cycle, we indexed the coercion a female received from all males, as the aggression she received from them between the onset of the mating season and the first day of her oestrous cycle. For each female, we also determined her 'top male coercer', as the male who coerced her the most before each oestrous cycle.

Quantifying social bonds

Female-male bonds (intersexual networks)

For each intersexual dyad, we calculated the rates of grooming (total duration of grooming recorded during focal observations divided by the total time of observation of the dyad) and proximity (number of scans a dyad was recorded in spatial proximity ≤ 5 m

divided by the total number of scans collected for the two members of the dyad), from the arrival of the male in the group until the beginning of the female's oestrous cycle. For grooming rates, we included only grooming given by the female to the male because male mandrills rarely groom females (MJEC unpublished data) and we considered this 'directed' rate to represent the effort invested by the female to maintain a bond with the male. For each female, we also determined her 'top male partner', as the male she groomed the most or the one with whom she was most often in spatial proximity from the beginning of the mating season to her first oestrous day. For each female and each mating season, we also calculated the grooming and proximity rates with the five males she groomed the most or she was most often in spatial proximity (Figure 3.2).

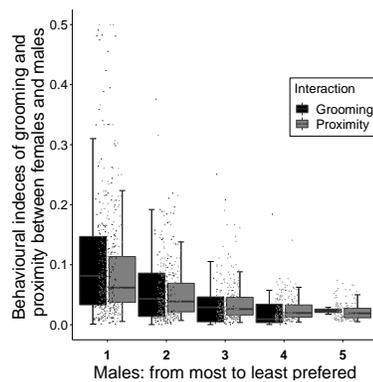


Figure 3.2: Distribution of grooming (black) and spatial proximity (grey) indices between each female and five males ordered from the highest to the lowest score for each mating season ($n=197$ female.seasons for the grooming index and $n=349$ for the proximity index). The grooming index corresponds to seconds that the dyad spent grooming divided by the seconds of observation of the dyad. The proximity index corresponds to the number of scans that the dyad was recorded in proximity divided by the total number of scans performed in the dyad. In each box, the middle, bottom and top line represent the median of the distribution and the 25th and 75th quartiles respectively.

We constructed intersexual social networks based on both grooming interactions and spatial associations because grooming interactions may better reflect affiliation bonds, while females may come closer to their male affiliates when they feel threatened by other males, even outside the resting periods, which are most favorable for grooming interactions. In grooming networks, the edges (connections) among adjacent individuals were directed (i.e. specified the direction of the grooming bout) and were weighted

by the total duration of grooming of the focal dyad. In the proximity networks, edges were weighted by the total number of scans for which the relevant dyad was recorded in proximity ($\leq 5\text{m}$).

We constructed one intersexual social network for each oestrous cycle of each female including all male-female interactions recorded between the onset of the mating season until the first day of the female's oestrous cycle. Affiliation networks may differ between seasons (birth vs mating) in seasonal breeders (Brent et al., 2013) like mandrills and thus, we considered the intersexual interactions during the mating season to reflect better the intersexual bonds that may influence mating patterns and potentially protect females from sexual coercion.

For each network, we computed each female's strength, calculated as the sum of weights of her edges. To standardize strength, we divided it by the total observation time of all males and the given female (for grooming networks) or by the total number of scans recorded on all males and the given female (for proximity networks).

Female-female bonds (intrasexual networks)

We constructed female social networks including only grooming interactions because grooming partners are likely to support each other in coalitions (Seyfarth and Cheney, 2012). We constructed one network in the 3-month time block, roughly equating to the last three months of each birth season of mandrills (January-March) for two main reasons. First, the birth season may be more appropriate to measure stable patterns of female-female social bonds, independently of sexual interactions and of the stress generated by the intense male-male competition and hierarchical instability following the arrival of males in the group at the onset of the mating season (Hamede et al., 2009; Wey et al., 2013; for mandrills see also: Beaulieu et al., 2017). Second, female social interactions recorded before the annual arrival of immigrant males are more likely to reflect the social landscape that these males face when entering the group and making decisions such as choosing which female to target.

We studied two classical social network metrics to measure a female's position in the intrasexual network: eigenvector centrality and strength (Ramos-Fernández et al., 2009).

Eigenvector centrality is a proxy of individual connectivity that takes into account indirect connections (i.e. connections mediated by third parties) by weighing every connection according to the centrality of the relevant adjacent individual (Bonacich, 2007). That is, an individual has a higher value of eigenvector centrality if it is connected to more central individuals (Ruhnau, 2000). Higher eigenvector centrality has been associated to higher dominance rank (Young et al., 2017) as well as survival and reproductive success (Vander Wal et al., 2015). Female strength was computed as the total duration of grooming she gave to, or received from, other female groupmates (sum of all inward and outward edges' weights for grooming networks). In contrast to intersexual grooming interactions, in female-female interactions, both individuals may offer grooming to each other and females may support both the females to whom they give or from whom they receive grooming. Females with high strength may enjoy fitness benefits (Silk et al., 2010b) and the strength of bonds may sometimes be a better predictor of fitness than overall connectivity (Schülke et al., 2010; represented here by centrality). We standardized strength in the female networks as in the intersexual networks.

We used the function *graph_from_data_frame* to create grooming and proximity networks and the functions *centr_eigen* and *strength* to compute eigenvector centrality and strength of each individual, respectively (R package *igraph*; Csardi and Nepusz, 2006).

Statistical Analyses

We first investigated the correlation structure of the different individual variables (age, rank, social variables) using pairwise Spearman's rank correlations to clarify which variables fit together in multivariate models (Figure S1). Higher ranking females enjoyed, on average, larger matriline (rho=0.36; Figure S1) but female rank was not correlated with any other proxy of intrasexual social bonds (Figure S1). Females with higher eigenvector centrality had also higher strength with other females in the intrasexual network (rho=0.5; Figure S1). All other pairwise correlations were non-significant.

Do females receive less coercion from males with whom they form stronger affiliation bonds (P1.1 vs P2.1)?

We ran a GLMM with negative binomial distribution to examine the determinants of variation in sexual coercion across intersexual dyads (response variable: number of aggressive events received). We considered the total focal observation time of the dyad (log-transformed) as an offset variable. We included the following explanatory variables: grooming rate of the heterosexual dyad during the period over which coercion was recorded, the difference between the male and the female's David's scores, the ages of the two individuals and their quadratic terms, and the operational sex-ratio. We included female and male identity as well as year of observation as random factors. We then re-ran this model including the proximity rate of the heterosexual dyad, instead of the grooming rate. We did not include grooming and proximity rate in the same model because they were correlated (Spearman's $\rho=0.38$, $p\text{-value}<0.001$; Figure S2).

Does a female's top grooming/social partner protect her against coercion from other males (P1.2 vs P2.2)?

We ran two GLMMs with negative binomial distributions to study the effects of male-female social bonds on the overall sexual coercion a given female receives from males. First, we tested whether sexual coercion received (response variable: number of aggression events received by a female from all males except her top grooming partner) is influenced by the outward grooming strength of the female with her top male grooming partner. We considered the total focal observation time of the female (log-transformed) as an offset variable. We also included the following control variables: female dominance rank, female age (and its quadratic term) and operational sex-ratio. We included female identity and year of observation as random factors. We then re-ran this model calculating, this time, both the response variable (male coercion) and the main explanatory variable (bond strength) based on the top male proximity partner rather than the top male grooming partner.

Does female integration in intersexual networks protect them against their main coercer (P1.3 vs P2.3)?

Second, we ran a model with a similar structure and the same offset, control and random variables but this time testing whether male sexual coercion (response variable: number of aggression events received by a female from her top male coercer) is influenced by the outward strength of the female with all the males in the grooming network except her top male coercer. We then re-ran this model by replacing outward grooming strength by the overall proximity strength.

Does female integration in intrasexual networks or the number of maternal kin in the group protect them against male coercion (P1.4 vs P2.4)?

We ran a GLMM with a negative binomial distribution to study the effects of female-female social bonds on the extent of sexual coercion a female receives from all males (response variable: number of aggression events received by a female from all males before her oestrous cycle). We used as main explanatory variable a female's eigenvector centrality. Otherwise, the structure of control variables (female rank, age and operational sex-ratio) and random effects was similar to the models described above (in P1.2 vs P2.2). Finally, we re-ran this model twice by replacing eigenvector centrality with (i) strength and (ii) matriline size.

We used R version 4.1.3 to run the above models with the function *glmmTMB* from the package *glmmTMB* (Brooks et al., 2017). We tested the significance of all fixed factors with the function *Anova* from package *car* (Fox and Weisberg, 2019) and we computed their 95% confidence intervals. We tested for multicollinearities with the function *cor.test* and we validated the models by testing the residual distributions, using the functions *testDispersion* and *testUniformity* from package *DHARMA* (Hartig, 2022).

Is the effect of female-female bonds on sexual coercion mediated by female attractiveness (P2.4a) or retaliation (P2.4b)?

We ran a mediation (path) analysis to test if females with higher eigenvector centrality in the intrasexual network receive more male coercion because they have on average higher reproductive success ('attractiveness hypothesis') and/or dominance rank ('retaliation hypothesis'; Figure 3.1). Similarly to other primates (Tinsley Johnson et al., 2014; Bray, Feldblum, and Gilby, 2021; Schülke et al., 2010), the three main variables in our path analysis (dominance rank, reproductive success and social bonds) are largely intertwined in mandrills (Charpentier et al., 2012; Smit, Huchard, and Charpentier, 2022) and our path analysis aims to overcome potential multicollinearities and disentangle the effect of these variables on sexual coercion. The intersexual dominance rank of the female and her reproductive success were not correlated (Figure S1); thus we could test them as potential mediators simultaneously to disentangle their effects (Kenny et al., 1998). In the same analysis, we specified, as above, female age and operational sex ratio as control predictor variables (Figure S3). The root-mean-square error of approximation (RMSEA) was ≤ 0.05 , the chi-square test was non-significant (p -value=0.424), the Comparative Fit Index was equal to 1.00 and the Tucker-Lewis Index was equal to 1.064, overall indicating good fit of the analysis (Steiger, 2007). We used R package *lavaan* (Rosseel et al., 2022) for the path analysis and the function *semPaths* from package *semPlot* (Epskamp et al., 2022) to illustrate it (Figure S3).

3.3 Results

Do females receive less coercion from males with whom they form stronger affiliation bonds (P1.1 vs P2.1)?

Grooming rates were positively correlated to coercion at the dyadic level, meaning that the most bonded dyads were also the most coercive (Figure 3.3a, Table 1). Similarly, in dyads characterized by higher proximity rates, males were more coercive ($\text{Chisq} = 26.190$, p -value <0.001 ; Figure 3.3a). Males in their prime were more coercive than younger and

older ones (Figure 3.3b; Table 1), confirming previous results (Smit, Huchard, and Charpentier, 2022). All other variables, including male-female power differential, indexed by their rank difference, were not significant (Table 1). Results were qualitatively similar when adding male rank and female rank as two explanatory variables instead of male-female rank difference (not shown).

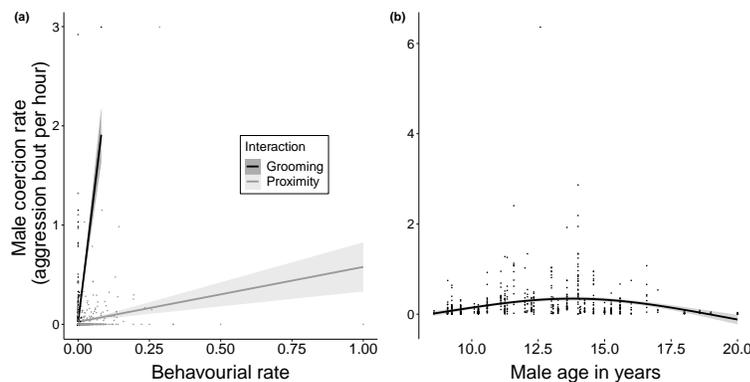


Figure 3.3: Drivers of variation in the intensity of sexual coercion within heterosexual dyads. Male coercion rate towards the female, as a function of (a) the affiliation rate of the dyad and (b) male age. Grooming rates correspond to the time spent (in seconds) by the female grooming the male divided by the total time of observation (in seconds) of each dyad. The proximity rate corresponds to the number of scans that the dyad was recorded in proximity divided by the total number of scans performed on the dyad. For graphical purposes, raw data are shown, regression lines are simple linear fits and shaded areas show 95% confidence intervals.

Does a female's top grooming/social partner protect her against coercion from other males (P1.2 vs P2.2)?

The intersexual bond with a female's top affiliation male partner did not protect her against coercion from other males. Instead, females who exchanged more grooming with their top grooming partner received more coercion from all other males (Figure 3.4a; Table 2b), while those who stood closer to their top proximity partner did not face more or less coercion from all other males ($\text{Chisq} = 0.360$, $p\text{-value} = 0.548$). Female rank, age and the operational sex ratio did not influence the results.

Does female integration in intersexual networks protect them against their main coercer (P1.3 vs P2.3)?

Females with stronger grooming bonds with all males except their top coercer did not receive more or less coercion from their top coercer than females with weaker bonds (Table 2a). In fact, there was an opposite, marginally non-significant trend of females who stood closer to all the other males receiving more coercion from their top coercer (Chisq= 2.753, p-value=0.097). Higher-ranking females received more coercion from their top coercer (Figure 3.4b; Table 2a) while female age and operational sex ratio did not influence the results.

Does female integration in intrasexual networks or the number of maternal kin in the group protect them against male coercion (P1.4 vs P2.4)?

We found that females who were more central (i.e. had higher eigenvector centrality) in the female grooming network faced more sexual coercion (Figure 3.4c, Table 3). Similarly, females with stronger bonds with other females in the grooming network received more coercion (Chisq=9.49, p-value=0.002) and this effect was qualitatively similar but marginally non-significant for females with larger matriline (Chisq=2.998, p-value=0.083; the effect was significant when female rank was not included given its correlation with matriline size; Figure S1; not shown). Moreover, there was a marginally non-significant trend for higher-ranking females to receive more coercion (Table 3). Finally, female age and the operational sex ratio did not influence the results.

Is the effect of female-female bonds on sexual coercion mediated by female attractiveness (P2.1) or retaliation (P2.2)?

The mediation (path) analysis revealed that the correlation between female-female social bonds (eigenvector centrality) and sexual coercion is independent from female repro-

ductive success or rank, failing to support the ‘attractiveness’ and the ‘retaliation’ hypotheses, respectively. In contrast, our results suggest that female-female social bonds directly influence the coercion a female receives, supporting the ‘public exposure hypothesis’. Finally, female rank and age appear to influence reproductive success but not sexual coercion (Figure S3; Table 4).

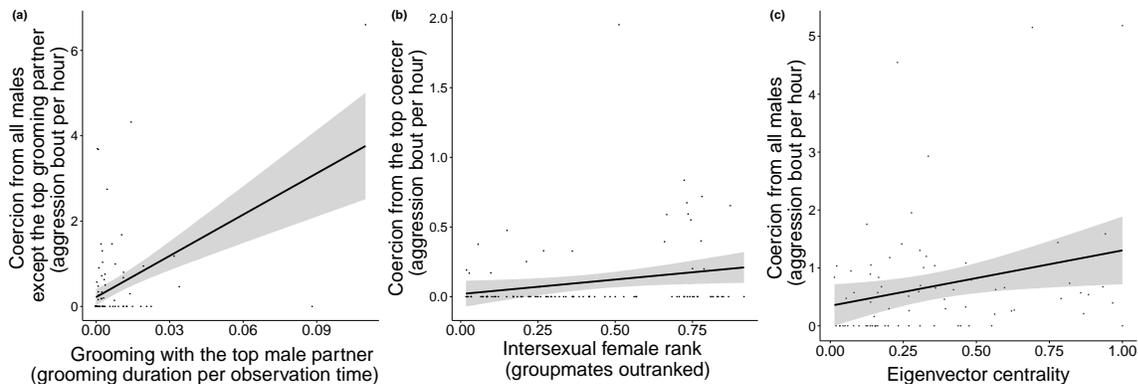


Figure 3.4: Drivers of variation in the intensity of overall male sexual coercion a female receives. (a) Male coercion received from all males except the top grooming partner as a function of the strength of the grooming bond of the female with him (grooming duration divided by the total time of observation). (b) Male coercion received from the top coercer as a function of the rank of the female. (c) Coercion received from all males as a function of the eigenvector centrality of a female in the female grooming network. For graphical purposes, raw data are shown, regression lines are simple linear fits and shaded areas show 95% confidence intervals.

3.4 Discussion

Driven by the well documented benefits of social bonds in several species including mandrills, we tested here whether social bonds are beneficial to females by protecting them from sexual coercion. We particularly investigated if females receive less coercion from males with whom they form stronger affiliation bonds (P1.1 vs P2.1), males protect their female partners against coercion from other males (P1.2 vs P2.2 & P1.3 vs P2.3) or females’ intrasexual bonds protect them against male coercion (P1.4 vs P2.4). Our results highlight that social context is a crucial factor mediating the expression of sexual coercion (Clarke et al., 2009) but contrary to our predictions, we found that females with stronger bonds

with either males or females receive more male coercion.

Our results first indicate that females who form stronger affiliative relationships with certain males, receive more coercion from these males. In other species, such as hamadrya baboons (*Papio hamadryas hamadryas*) males coerce mostly their female partners presumably in order to force females to maintain proximity with them and to reduce the chances that they will mate with surrounding rival males (Swedell and Schreier, 2009). Similarly, male bottlenose dolphins (*Tursiops aduncus*) aggressively enforce proximity with females (King et al., 2019), suggesting altogether that females might be coerced into associations with/from coercive males and that the observed social bonds are in fact an outcome of male coercion. Conversely, female-male associations might be characterized de facto by high levels of male coercion due to increased proximity of the heterosexual dyad. However, this last hypothesis is at odds with certain empirical evidence. First, a continuously growing body of research suggests that animal groups are rather highly socially structured and the social environment of an individual is unlikely to be random, but instead reflects the existence of highly differentiated relationships between group members (Lusseau, 2003; Croft et al., 2005). Second, in other species, like chacma baboons, which are closely related to mandrills and males also use sexual coercion (Baniel, Cowlshaw, and Huchard, 2017), females often form non-aggressive associations with certain males characterized by high spatial proximity (Palombit, Seyfarth, and Cheney, 1997; Baniel, Cowlshaw, and Huchard, 2016). Hence, the increased male coercion within more bonded heterosexual mandrill dyads is unlikely to result solely from variation in spatial proximity. Finally, in humans where intimate partner violence and sexual coercion are widespread (Basile, 2002), male sexual jealousy represents the most common cause for wife beating (Smuts, 1992). Similar functions of jealousy, to retain a valuable social bond against potential intruders (Hart and Legerstee, 2010) has been previously reported in primates and other mammals across different contexts (i.e. not only sexual; Tutin, 1979; Hart and Legerstee, 2010; Webb et al., 2020; Harris and Prouvost, 2014). Therefore, the increased coercion rates of male mandrills towards their female partners may also be influenced by relevant mental states of males, when their bond is threatened by rival males.

We further found that females with stronger affiliation bonds with all males do not re-

ceive more or less coercion from their main coercer. Previous studies on baboons suggest that intersexual affiliation may provide protection for females and their infants in the context of male-female stable heterosexual associations (Palombit, 1999). However, similar protection may not exist for females against coercive partners, or may exist in baboons but not mandrills. In the first case, baboon stable heterosexual associations are typically formed once a female has conceived with a male (Baniel, Cowlshaw, and Huchard, 2016) and are most intense once the infant is born (Palombit, Seyfarth, and Cheney, 1997; Palombit, Cheney, and Seyfarth, 2001) but there is currently no evidence that males protect their female partners against coercion by other males after weaning their babies. In the second case, female mandrills do not appear to form such stable heterosexual associations (Figure 3.2) and thus, males are more unlikely to protect females, at least in respect to sexual coercion. The seasonal emigration of male mandrills may limit the duration of female-male relationships (e.g. to one mating season) in comparison to species where males are permanent residents, and thus, male mandrills may not gain any substantial benefits from protecting their mating partners against other males. In addition, given that the highest-ranking male mandrills are most coercive (Smit et al., 2022), other males would likely face high risks when confronting coercive males to protect their female partners.

We found also that females with stronger grooming bonds with their top grooming partner receive more male coercion from all other males, which is harder to interpret. This result may reflect that females who are more integrated in heterosexual networks are also the most coerced, either because they are more exposed or more attractive, or because the females who are most coerced may groom coercive males in an appeasement strategy (Baniel et al., 2021). Alternatively, such relationship may reflect a male competitive strategy, where males aim to reduce the mating success of their rivals by intimidating their female partners or to provoke aggressive confrontations that they are likely to win, similarly to other species where high-ranking males may attack the female associates of lower ranking males (Smuts, 1985). In addition, by assaulting females who preferentially maintain proximity to lower ranking males, high-ranking males may disrupt the association of the female with the other male and prevent female from expressing mate choice (Manson, 1991). Overall, it's clear from these results that males do not provide any form of protection to the females, but less clear why male-female associations may

expose females to more coercion.

Although previous evidence from other mammals shows that female social integration may reduce coercion by males, our results suggest that more bonded female mandrills receive more male sexual coercion and these results remained qualitatively similar when we used different proxies of social bonds (centrality, strength or matriline size), ruling out the possibility of a methodological artifact. A recent study in rhesus macaques found no evidence that grooming is exchanged for coalitionary support, i.e. grooming partners do not appear to have higher probability to support each other in conflicts (O’Hearn et al., 2022). Therefore, the association of social bonds with sexual coercion in mandrills may be independent of social support and this may explain why social bonds are not protective. However, this is not sufficient to explain why social bonds are associated with more coercion. Our mediation (path) analysis did not show any support for the ‘attractiveness’ or ‘retaliation hypothesis’, i.e. more bonded females did not receive more coercion because they were attractive or more powerful and retaliate more against males and if the effect of social bonds on sexual coercion is mediated by retaliation or reproductive success, it is with an intensity below the ability of our analysis to detect it. Instead social bonds appear to have a rather direct effect on coercion, potentially reflecting that females who are more bonded, are more involved in the social life of the group and interact more with other groupmates including coercive males (‘public exposure hypothesis’). In addition, such interpretation is supported by our results as a whole which suggest that more bonded females, either with males or with other females, receive more male coercion. Altogether, these results are at odds with results in other species. For example, peripheral female brown capuchin monkeys (*Cebus apella*; Janson, 1990) receive in general more aggression while social isolation (and not integration) is associated with higher risk of sexual harassment in humans (Cense and Brackenridge, 2001).

Our results add to a handful of studies suggesting that social bonds may be associated with certain costs. For example, both female and male prairie voles (*Microtus ochrogaster*) have higher mating success when they have an intermediate (rather than high) number of social connections (Sabol et al., 2020) and affiliation bonds are associated with reduced offspring survival in female eastern grey kangaroos (*Macropus giganteus*; Menz et al., 2020) and reduced longevity in yellow-bellied marmots (*Marmota flaviventris*; Blumstein

et al., 2018) and blue monkeys (*Cercopithecus mitis stuhlmanni*; Thompson and Cords, 2018). However, these examples constitute exceptions and in most species, social bonds are associated mostly with (fitness) benefits (Snyder-Mackler et al., 2020) such as increased longevity or survival of adults and infants (Silk et al., 2010b; Stanton and Mann, 2012) and reproductive success (Gerber et al., 2022). In mandrills, more bonded females enjoy documented fitness benefits Charpentier et al., 2012 while the increased coercion levels that they receive are not formally associated with fitness costs, despite the increased injury risk that coerced female mandrills face (Smit et al., 2022). In addition, even if females in mandrills or other species face certain costs due to male coercion, such costs might be ephemeral, i.e. concentrated during the period before conception when the female is coerced by males. Conversely, the benefits of social bonds across different species might be long-lasting and independent of the life stage or reproductive state of females and overall, they seem to counterbalance the potential costs and to increase the adaptive value of social bonds.

In line with the original study documenting the expression of sexual coercion of male mandrills, our study suggests that high-ranking females in general receive more male coercion than low-ranking females (Smit et al., 2022). In addition, our results show that this effect is independent from the effect of social bonds on sexual coercion and indicate that the benefits or costs of social bonds can be independent of dominance rank (for an example of independent benefits see: Silk, Alberts, and Altmann, 2003) despite the correlation of these two traits in several species (Vullioud et al., 2019; Wooddell, Kaburu, and Dettmer, 2020). This result may reflect that in large animal groups, like mandrill groups which often count hundreds of individuals (Abernethy, White, and Wickings, 2002), females may have the latitude to form multiple and/or strong social bonds with groupmates regardless of their rank. Nevertheless, female rank did not influence the aggression a female received from all males except her top grooming partner; presumably because this aggression does not reflect (only) sexual coercion but also, as mentioned above, male-male competition and it is therefore independent from the traits of females. Finally, the lack of correlation of the rank difference of the heterosexual dyad with the coercion the dyad male addressed to the dyad female may reflect that power asymmetries between coercive males - which often are the highest-ranking ones (Smit et al., 2022) - and their targets are so large anyway that the actual value of the rank difference between

one particular male and one particular female does not change much.

Our results clearly show that social bonds with males or females are not protective against sexual coercion for mandrill females; these results call for further investigations in other societies, in order to start understanding the social ecology of sexual coercion, and whether the social environment can, at least in some cases, mitigate the risks of coercion faced by females. They further suggest that female mandrills may experience trade-offs between the benefits they get from their affiliation bonds with males and females, and the costs such bonds may generate, such as greater exposure to sexual coercion. Future work should shed some light on the relative fitness costs and benefits of these females who are more socially connected, which may not be of comparable magnitude. More generally, studies in sexually coercive species should investigate the fitness costs of sexual coercion suffered by females as well as the mechanisms allowing them to gain more reproductive control.

3.5 Supplementary figures

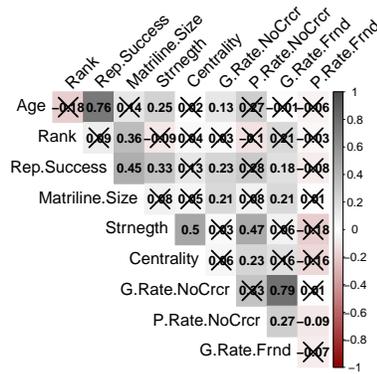


Figure S1. Spearman’s rank correlations of the main variables. Non-significant correlations are represented by crossed out tiles and significant correlations are represented by the corresponding Spearman’s rank correlation rho. White tiles represents absence of correlation, black tiles represent positive and red negative correlation (the darker colours correspond to stronger correlation).

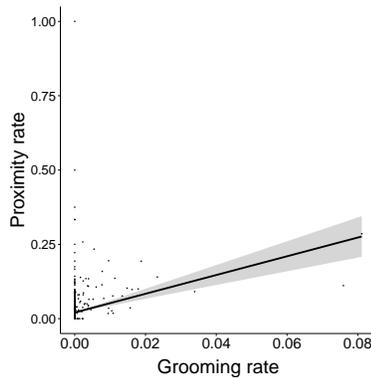


Figure S2. The relationship between the grooming rate and the and proximity rate between the two members of a heterosexual dyad within a mating season: from the arrival of the male in the group until the beginning of the female’s oestrous cycle. The grooming rate equals the total duration of grooming recorded during focal observations divided by the total time of observation of the dyad. The proximity rate equals the number of scans in which a dyad was recorded in spatial proximity $\leq 5m$ divided by the total number of scans collected for the two members of the dyad. The Spearman’s rank correlation coefficient and the relevant p-value are shown.

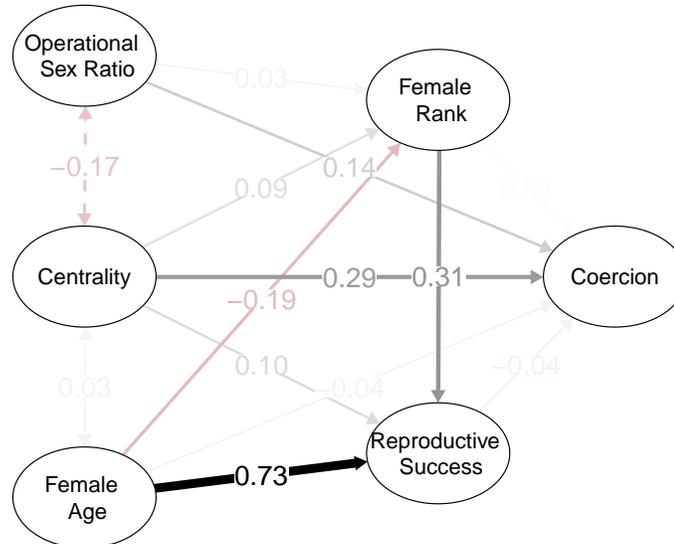


Figure S3. Path diagram illustrating the direct and indirect (mediated by female reproductive success and dominance rank) effects of eigenvector centrality in the female intrasexual network on the coercion a female receives from all males. The relationships between other variables are also shown. Edge width and opacity are scaled to standardized estimates. Edge colour represents positive (black) or negative (red) relationship. The causal relationships implied are based on working hypotheses.

Authors' Contributions: N.S., E.H. and M.J.E.C. designed the study; N.S performed the statistical analyses and wrote the first version of the manuscript; All authors contributed to writing the manuscript; M.J.E.C. and N.S. contributed to data collection and database management.

General Discussion

Sexual conflict is common in polygynous or polygynandrous species where intrasexual competition is high, leading often to the evolution of sexual dimorphism and male superiority in size and strength (Emlen and Oring, 1977). This physical superiority may help males to constrain females' mating behaviour to comply to their will (Smuts and Smuts, 1993). Hence, the expression of sexual coercion in mandrills (*Chapter 2*) which are highly sexually dimorphic and live in large polygynandrous groups was not unforeseen. However, the results in *Chapters 1 & 3* emphasize that female mandrills have some power over, at least some, adult males and that the intensity and effect of sexual coercion is not equally distributed among all females, but high-ranking and more socially bonded females receive more male coercion.

The following discussion presents these results in a broader context to assist in the current understanding of social and reproductive struggles among the sexes in polygynandrous species. First, the context-dependence of intersexual dominance in mandrills is discussed with a particular attention given to the role of social integration. Then, the link between dominance and sexual coercion is described by examining the influence of dominance on sexual conflict. The expression of sexual coercion, and particularly sexual intimidation, by male mandrills is then discussed in the general framework of the different forms of coercion and their ecology, i.e. the conditions which facilitate each form and its influence on the different social and reproductive system. The costs that females face due to male coercion are also described and given the constraints that male coercion impose on female mate choice, the behavioural strategies or physiological adaptations that may help females to avoid these constraints are presented. Finally, the trade-offs that female mandrills appear to experience between male coercion and social bonding are contrasted

with the adaptive value and the beneficial role of social bonds in many species including mandrills.

The dynamic landscape of intersexual dominance

Most studies so far have traditionally categorized species as strictly male or female dominant but *Chapter 1* adds to a few recent studies which draw a more nuanced landscape where intersexual dominance varies along a full spectrum between these two extremes (Hemelrijk, Wantia, and Isler, 2008; Hemelrijk et al., 2020; Izar et al., 2021; Kappeler et al., in press). Female mandrills can hold some power over males even if they generally submit to them and the intrasexual rank of an individual of either sex can predict its intersexual rank and the intersexual hierarchy represents an interdigitation of the male and female intrasexual hierarchies (see also: Kappeler et al., in press). Hence, in polygynandrous animal groups the social competition within and between the sexes might be demonstrated through similar agonistic interactions and the construction of intersexual dominance hierarchies may represent a more complete image of the social landscape of multimale-multifemale social groups than the two intrasexual hierarchies.

Intersexual dominance is context-dependent

The prediction in *Chapter 1* that female mandrills may hold leverage related power over males was based on the recent relevant literature which suggests that female power may reflect leverage more than dominance *sensu stricto* (Lewis, 2020). Nonetheless, the absence of evidence suggesting that female mandrills hold such leverage (indexed here by the probability of females to win more intersexual conflicts when they are sexually receptive) is not surprising. Females may have leverage related power, when they can control their reproductive activity, like in several species of lemurs where females can overpower males (Dunham, 2008; Norscia and Palagi, 2015; Hohenbrink et al., 2016; Lewis, 2020; Lewis, Bueno, and Di Fiore, in press) and males may avoid conflicts with them (Lewis, 2002). In addition, previous findings underline an association of female-biased power with sexual size monomorphism (e.g. spotted hyenas (*Crocuta crocuta*): Vullioud et al., 2019; primates: Ferrari, 2009; Petty and Drea, 2015) while male-biased dominance

is associated with male-biased sexual size dimorphism (Kappeler, 1993). Therefore, in species characterized by male biased sexual size dimorphism and sexual coercion like mandrills (Setchell et al., 2001; *Chapter 2*) or their close relatives chacma baboons (Barrett and Henzi, 1997; Baniël, Cowlshaw, and Huchard, 2017), the extent of female reproductive control is expected to be low meaning that females cannot use access to sex as leverage to increase their power. Indeed, chacma baboons show strict male dominance over females (Kalbitzer et al., 2015). Female mandrills, however, appear to occasionally dominate certain males with an average female outranking one out of ten males.

Female mandrills outrank more males during the mating season although they direct more aggression towards males during the birth season. This increased aggression rate during the birth season is similar to Japanese macaques (*Macaca fuscata*; Schino, D'Amato, and Troisi, 2004) and humans (Hahn-Holbrook et al., 2011) where females are more aggressive while lactating their infants. The higher energetic demands that females face due to gestation and lactation (Dunham, 2008) and the presence of dependent infants may motivate females to assault males more during the birth (vs. mating) season, first in order to secure food and second to protect their infants from male attacks. Accordingly, in Columbian ground squirrels (*Spermophilus columbianus*), females show greater dominance over males while lactating (Murie and Harris, 1988).

Instead of leverage, the increased female dominance during the mating season may simply reflect the demographic changes due to immigration of newcomer males during this season, a hypothesis supported further by the fact that the sex-ratio also influences intersexual dominance. In particular, female mandrills outrank more males when more males are present in the group, meaning most likely that male-male competition is more intense and there is a larger number of males which are located low in their intrasexual hierarchy. First, these subordinate males may not dominate females because they adopt alternative reproductive strategies than sexual coercion and thus, they may be less aggressive towards females in order to solicit them in sneaky copulation and avoid the intervention of more dominant males. Accordingly, in rock hyraxes (*Procapra capensis*), low-ranking immigrant males try to sneakily copulate rather than entering the contest arena of high-ranking resident males (Bar Ziv et al., 2016). In addition, examples of adaptation of male mating strategies depending on the social context include also the young

male reindeer (*Rangifer tarandus*), that increase their reproductive effort when powerful prime-aged males are not present (Mysterud et al., 2003) and red deer (*Cervus elaphus*) where even prime-aged males decrease their reproductive effort when more males are present in their group (Yoccoz et al., 2002).

Second, the increased number of males during the mating season may generate ‘winner-loser effects’. A loser effect means that a history of losing makes an individual more likely to lose future contests (Dugatkin, 1997; but see also: Bonabeau, 1999). The increased intensity of male-male competition during the mating season because of male motivation for mating, may therefore result in an increased number of (injured) male ‘losers’ who may eventually submit further to females (Hemelrijk, Wantia, and Isler, 2008; Bonabeau, 1999). Third, in several species, where members of one sex immigrate and enter at the bottom of the hierarchy in their new groups, group tenure is highly associated with dominance rank (e.g. female great apes: Robbins et al., 2005; Foerster et al., 2016; or male macaques: Berard, 1999; Takahashi, 2002; and spotted hyenas: East and Hofer, 2001). New immigrant male mandrills may enter low in the hierarchy and may have a higher probability to be outranked by females shortly after their arrival in the group during the mating season before they rise in the hierarchy.

Social integration impacts intersexual dominance dynamics

The association of seasonal immigration patterns of male mandrills with their occasional domination by females is further supported by the effect of male social integration on dominance rank (*Chapter 1*). In particular, when a given male mandrill forms more social bonds with females, he has a higher probability to dominate a given female, while peripheral males with weak social connections are more likely to be outranked by females. Because immigrating males are often unfamiliar to females of the group, they may need time to integrate socially after their arrival during the mating season; and in the meantime females outrank them. Similarly, in vervet monkeys - where females have likely more reproductive control than female mandrills which are sexually coerced - females can improve the dominance rank of their preferred males through social integration (Young et al., 2017; Bonnell et al., 2020). This way females can bypass the constraints on their reproduction imposed by male-male competition and particular by the

high-ranking males (Young et al., 2017). Therefore, although intrasexual male dominance rank is mostly determined through physical contests in mandrills (Setchell, 2016), these results suggest that females may have some extent of social control over male dominance status.

Similarly to males, more socially integrated female mandrills in the female social network dominate more males than females with limited social connections. In line with this, dominance rank and social connections are highly associated in geladas (*Theropithecus gelada*; Tinsley Johnson et al., 2014). The observed formation of occasional female mandrill aggressive coalitions against males (Setchell, Knapp, and Wickings, 2006; personal observation) may further highlight the benefits of social bonds and the latitude these bonds offer to females, for example, to retaliate against physically superior males. Such female-female coalitions against assaulting males are also observed in geladas (Dunbar, 1975) and Guinea baboons (*Papio papio*; Goffe, Zinner, and Fischer, 2016) which are closely related to mandrills and their intersexual agonistic interactions are less male dominated than, for example, in chacma baboons (Kalbitzer et al., 2015). Hence, female coalitions may play an important role in the evolution of female empowerment, a hypothesis supported also by their critical role in the establishment of intersexual dominance in certain species where female dominance is pronounced (spotted hyenas: Vullioud et al., 2019; bonobos: Parish, De Waal, and Haig, 2000). Altogether, female philopatry, social bonds and support may offer some power over males, even in species like mandrills where male dominance is the norm and males are significantly physically superior to females.

Dominance rank is a decisive factor in sexual conflict

Across different taxa, the social relationships and particularly the dominance status of an individual within a social group may provide it with a variety of fitness benefits like higher reproductive success (Ellis, 1995). In primates, for example, both females and males of higher dominance rank have greater fecundity than subordinate individuals (Majolo et al., 2012). Dominance rank may also determine the partitioning of reproduction and freedom to express mate choice (Keller and Reeve, 1994), i.e. to increase the

reproductive control of an individual, and to offer to dominant individuals the power to constrain the reproduction of subordinate ones in order to increase their own fitness (Clutton-Brock, 2007). Similarly, when males are dominant over females, the latter have low reproductive control and thus, male monopolisation potential is high (Davidian et al., 2022; see also: Figure 5). The results presented here suggest that dominance is a crucial component of the mandrill mating system and influences the operation of sexual selection both within and between sexes.

Male rank. Empirical evidence from species of different taxa suggests that the determining influence of dominance rank in reproductive success is likely stronger in males than in females (Ellis, 1995). In line with this, male mandrills show a high reproductive skew in favour of the alpha males who monopolise 60-70% of reproductions (Charpentier et al., 2020; Charpentier et al., 2005). The results in *Chapter 2* suggest that alpha male mandrills also copulate more and they are more coercive than subordinate males. Therefore, sexual coercion seems to be a selected male reproductive strategy that may increase male reproductive success similarly, for example, to chimpanzees (Feldblum et al., 2014). Sexual coercion may be an efficient strategy for powerful males, but weak males, that are occasionally outranked by females in mandrills, may adopt, instead, different mating strategies as mentioned earlier. Consequently, although females can outrank some males, these males may not be the ones who coerce them sexually and such partial female empowerment may have a negligible consequence on the reproductive outcomes or the latitude of females to express mate choice.

These results are at odds with evidence from other species where subordinate males are often more coercive (Boeuf and Mesnick, 1991; Kunz et al., 2021b). This difference may emerge from the fact that male dominance status can impact the expression of male coercive strategies differently, depending on the social organization and female-male interaction patterns of different species. In polygynandrous societies, where several males are present in a group, subordinate males may be generally excluded from mating opportunities and may not coerce females in order to avoid the intervention of dominant males. As suggested from mandrills, in such societies, dominant males may use (long-term) coercion to constrain female promiscuity and impose closer proximity taking advantage of long-lasting female-male associations. In contrast, in solitary species, where intersexual

associations are not long-lasting, females are unlikely to be defended by dominant males, and therefore subordinate males may use short-term coercive strategies (harassment or forced copulation) to increase their mating success whenever they have the opportunity (Clutton-Brock and Parker, 1995b). In orangutans, a solitary species, for example, females show a preference for dominant (flanged) males (Knott et al., 2010) and may resist more and receive more coercion (forced copulation) from subordinate males (Kunz et al., 2021b). Nevertheless, an example at odds with the assumed relationship of male dominance rank, coercion and social organization comes from pinnipeds, where females may be harassed more often by satellite (subordinate) males (Cappozzo, Túnez, and Cassini, 2008), potentially because these males want to mate fast before the dominant male who protects the group intervenes. Altogether, social organization seems to influence the relationship of male dominance rank with the rates (and forms) of sexual coercion across species, but more factors may impact this relationship.

Female rank. In comparison to low-ranking females, high-ranking female mammals often have shorter inter-birth intervals and their infants mature faster and have higher probability of survival (Pusey, Williams, and Goodall, 1997; Côté and Festa-Bianchet, 2001). Similarly, high-ranking female mandrills have overall higher reproductive success than subordinates (Setchell et al., 2002; Dezeure, Charpentier, and Huchard, 2022). Male mandrills prefer to mate with high-ranking females (Setchell and Jean Wickings, 2006) and this may explain why they also coerce high-ranking females more often than low-ranking ones. Namely, males may prefer coercing and mating with females that have greater chances to reproduce successfully and/or faster. Such male preference for females with higher reproductive qualities has been documented in other mammals such as spotted hyenas (Szykman et al., 2001) and several primates (Keddy-Hector, 1992; Muller, Thompson, and Wrangham, 2006; Pusey, Williams, and Goodall, 1997). Alternatively, the observed increased coercion towards high-ranking females may reflect the greater physical effort that males need to make in order to impose their mating choice on these females who are more powerful and can outrank more males in comparison to low-ranking ones.

High-ranking female mandrills receive more male aggression regardless of their reproductive state, including pregnant and early lactating females which are not potential mating partners for males the coming period (*Chapter 2*). Therefore, male sexual coer-

cion may not be sufficient to explain the bias of male aggression towards high-ranking females in and of itself. Instead, males may need to assault powerful females more also because it is harder for them to subdue them socially. Empirical evidence from both birds (Jonart, Hill, and Badyaev, 2007) and mammals (Clutton-Brock and Albon, 1979) suggest that contests are more common between individuals with smaller asymmetries in power; hence, high-ranking female mandrills which have a smaller power differential with males, may compete with them for social power while low-ranking females may submit socially to males easier.

The ecology of sexual coercion

Sexual coercion can have a strong influence on the social landscape of an animal population. Infanticide can impact population sizes in certain mammals like African lions (*Panthera leo*; Whitman et al., 2004) and sexual harassment can shape the social network of fishes, by reducing the level of association of harassed females (e.g. guppies (*Poecilia reticulata*): Darden et al., 2009) or can lead to sexual segregation in bottlenose dolphins (*Tursiops aduncus*) with females avoiding groups with males (Galezo, Krzyszczyk, and Mann, 2018). Sexual coercion can particularly impact the evolution of mating and social systems of several animals (Thornhill, Alcock, et al., 1983; Smuts and Smuts, 1993; Clutton-Brock, 2021) including humans (Smuts, 1992; Stumpf et al., 2011). Females from certain mammals, for example, group around dominant males, seeking protection from them against other males but also benefiting from a dilution effect of sexual coercion, when an increased number of females leads to less coercion for an individual female (Cassini, 2021). Relevant examples come from pinnipeds where male coercion promotes female gregariousness (Cappozzo, Túnez, and Cassini, 2008) and ungulates where sexual harassment has been suggested to exert a selective pressure for the evolution of lek breeding (Clutton-Brock, Price, and MacColl, 1992; Nefdt, 1995). This social response of females to male coercion may have further influenced the evolution of polygyny in mammals through a positive feedback loop (Figure 5): First, female aggregation to avoid male coercion can facilitate male monopolisation strategies. Male monopolisation, in turn, can amplify male-male competition and increase male reproductive skew in favour of dominant males. Then, male-male competition may promote male biased sexual size

dimorphism that facilitates the expression of sexual coercion, since male physical superiority reduces the costs of intersexual aggression for males. Finally, the loop is completed when male sexual coercion further promotes female aggregation and polygyny (Cassini, 2020; Figure 5). Empirical studies indicate indeed that sexual coercion occurs most often in sexually dimorphic species (of different orders: primates, even- of odd-toed ungulates including cetaceans, and carnivores) with pronounced levels of polygyny (Cassini, 2021).

The sexual dimorphism, the high levels of polygyny and the results of this work indicating that male mandrills use sexual coercion against females conform with the observations described in the previous paragraph. Male mandrills appear, in particular, to use sexual intimidation, i.e. aggression over long time periods preceding a female's receptive period, in order to increase their mating success with their female victims. Conversely, the use of other coercive strategies such as sexual harassment and punishment, are not supported by the results. Male mandrills use a wide repertoire of aggressive behaviours to intimidate females, including threats (such as head-bob or ground-slap) which produce little immediate behavioural reactions in the victims. This result suggests that the extreme physical superiority of male mandrills may allow them to use lower aggression severity to intimidate females. This may apply also to other species but previous studies in sexually dimorphic species that use sexual intimidation have analysed only patterns of severe male aggression towards males (Muller et al., 2007; Baniel, Cowlshaw, and Huchard, 2017).

The use of a long-term coercive strategy from male mandrills, is in line with the of this species. In species where female-male associations are ephemeral, males may use more often short-term coercive strategies which increase their immediate mating success with the victims (Smuts and Smuts, 1993; Clutton-Brock and Parker, 1995b). Conversely, in species which live in relatively stable multimale-multifemale groups, like mandrills, males can use long-term coercive strategies such as sexual intimidation or punishment (Smuts and Smuts, 1993; Clutton-Brock and Parker, 1995b). Despite the long-term intersexual associations, however, mandrills are promiscuous and they do not seem to form exclusive mating bonds outside mate-guarding episodes while females can potentially escape male monopolisation strategies in their dense habitat and sneakily mate with other males (Setchell and Kappeler, 2003; personal observation). Hence, the absence of male

sexual punishment of females that copulate with other males is not surprising. By contrast, sexual punishment is documented, for example, in geladas which live in more open habitat than mandrills (le Roux et al., 2013) and one leader male can aggressively control sexual access to females from his unit (Snyder-Mackler, Alberts, and Bergman, 2012).

To date, sexual intimidation has also been reported only in chimpanzees (Muller et al., 2007) and chacma baboons (Baniel, Cowlshaw, and Huchard, 2017). Although male violent aggression resulting in serious female injuries is probably less common in mandrills than, at least, in chacma baboons (Baniel, Cowlshaw, and Huchard, 2017), the rates of severe male aggression towards females in mandrills appear to be higher than in chacma baboons (Baniel, Cowlshaw, and Huchard, 2017) and similar to chimpanzees (Muller et al., 2007; Watts, 2022). This relatively high frequency of female directed aggression may reflect the effect of reproductive seasonality and male immigration on the mating behaviour of mandrills. Male mandrills may have less time than male chimpanzees or chacma baboons - which are not seasonal breeders - to secure mating and establish (coercive) relationships with females. Hence, they concentrate all their effort in the few weeks or months between their immigration in the group each year and the female receptive periods. Altogether, despite such differences, the common characteristics of these three species (chimpanzees, chacma baboons and mandrills) may suggest that sexual intimidation is a form of sexual coercion more common in polygynandrous and/or sexually dimorphic mammals than previously thought (Cassini, 2020) and the temporal uncoupling of male aggression and mating as well as the long-term observations needed for the study of sexual intimidation may explain the scarcity of detailed studies on this topic.

Why sexual coercion evolved if it is costly for females?

Constraints imposed by male mating strategies may largely impact female fitness across different taxa (Cassini, 2000) and females may face fitness costs because they can not exert mate choice (Smuts and Smuts, 1993; van Schaik, Pradhan, and van Noordwijk, 2004; Clarke et al., 2009). Male sexual aggression may also impose more direct costs to females that include increased energy expenditure (Watson, Stallmann, and Arnqvist, 1998) and decreased reproductive success (Gay et al., 2009; den Hollander and Gwynne,

2009; Rossi, Nonacs, and Pitts-Singer, 2010; Takahashi and Watanabe, 2010) in insects, reduced short-term female fitness in fishes (Magurran and Ojanguren, 2007) and injury or even death in birds (McKinney and Evarts, 1998). Female mammals can face equally high, if not higher, costs. Most strikingly, males may kill previous infants of females in order to make females resume cycling and to increase their own reproductive outcomes (Lukas and Huchard, 2019). Female pinnipeds may get injured (Boeuf and Mesnick, 1991; Hiruki et al., 1993) and feral sheep may die as a consequence of male harassment (Réale, Boussès, and Chapuis, 1996). Milder consequences may include ecological costs, like in bottlenose dolphins (*Tursiops truncatus*) where females avoid preferred habitats when they are aggressively sequestered by male alliances (Wallen et al., 2016). In primates, previous studies have demonstrated that male coercion is associated to injuries (Baniel, Cowlshaw, and Huchard, 2017; for evidence in humans see also: Novak and Hatch, 2009), increased stress levels (Muller et al., 2007) and ecological or energetic costs (Kunz et al., 2021a; Watts, 2022) for females. Sexually coerced female chimpanzees, for example, may exhibit increased cortisol levels (Muller et al., 2007) and refrain from feeding, remaining stationary high in the canopy, for long periods of time (Watts, 2022).

Female primates are characterized by low fertility (Jones, 2011) and high energy allocation to each offspring (Gittleman and Thompson, 1988) in comparison to most animals. As a consequence, the costs of sexual coercion and failure to express mate choice, i.e. mate with quality mates and produce offspring with ‘good genes’, may be higher than in other animals. Altogether, the costs of male aggression and sexual coercion seem widespread across primates and other animals and a question emerges regarding the adaptive value of sexual coercion given these costs. Male coercion is likely to inflict injuries on female mandrills (*Chapter 2*) which, in turn, can potentially bring upon further costs such as energetic expenditure for healing or mortality risks. The combination of these results with the fact that female mandrills can influence male dominance status and that alpha males are more coercive, highlights a second question: if females can influence the identity of the males with whom they mate and reproduce more, why do they receive the most sexual coercion from them?

Females are expected to aim reducing the costs of male coercion and hence, if they can choose their mates, they should avoid choosing based on male physical strength (e.g. ar-

maments) which may facilitate male coercion. More generally, when male-male competition operates in opposite direction than female mate choice and promotes male traits that do not reflect male mate quality or they are harmful for females, females are not expected to use cues like aggression or dominance to choose their mates (Qvarnström and Forsgren, 1998). Instead, they should use other cues such as visual (e.g. ornaments), chemical (Penn and Potts, 1998) or acoustic (Searcy and Andersson, 1986) traits. Observations of mandrills complicate the study of this hypothesis. In particular, the extreme colouration of males (potentially selected through female choice; Setchell, 2005) in combination with their physical superiority and coercive nature underline the multilevel function of sexual selection and a potential arms race among the sexes.

The physical differences between mammals and birds may help to elucidate the evolutionary roots of sexual coercion. In mammals, male weaponry is often extravagant and sexual coercion potentially more common than in birds where ornaments - rather than armaments - usually mediate mate choice (Devlin Calkins and Tyler Burley, 2003; Pradhan and Schaik, 2009). The movement of female birds may be de facto less restricted than (terrestrial) mammals and the male monopolisation potential might be lower in birds (Pradhan and Schaik, 2009). As a consequence, the increased body size and physical power which would allow sexual coercion of females may not be as beneficial to male birds as in mammals where males can constrain female movement and impose their mating choice (Caizergues and Lambrechts, 1999). Therefore, the relative importance of male-male competition that promotes male physical strength in comparison to female mate choice, may be greater in mammals than in birds.

Another possible explanation for the evolution of sexual coercion is based on the fact that females usually constitute the limiting sex because in contrast to males they can produce only one offspring (or litter etc.) at a time (Darwin, 1871). This limitation may intensify male intrasexual competition for access to mates which can reinforce the aforementioned feedback loop (Figure 5) in an earlier stage, i.e. to promote sexual size dimorphism which then can influence the appearance of sexual coercion. Females can potentially balance, at least partially, the costs imposed from coercive males by producing (sexually coercive) male offspring with higher reproductive success ('sexy son hypothesis'; Fisher, 1915) but given that male coercion may result in impregnation by non-preferred males,

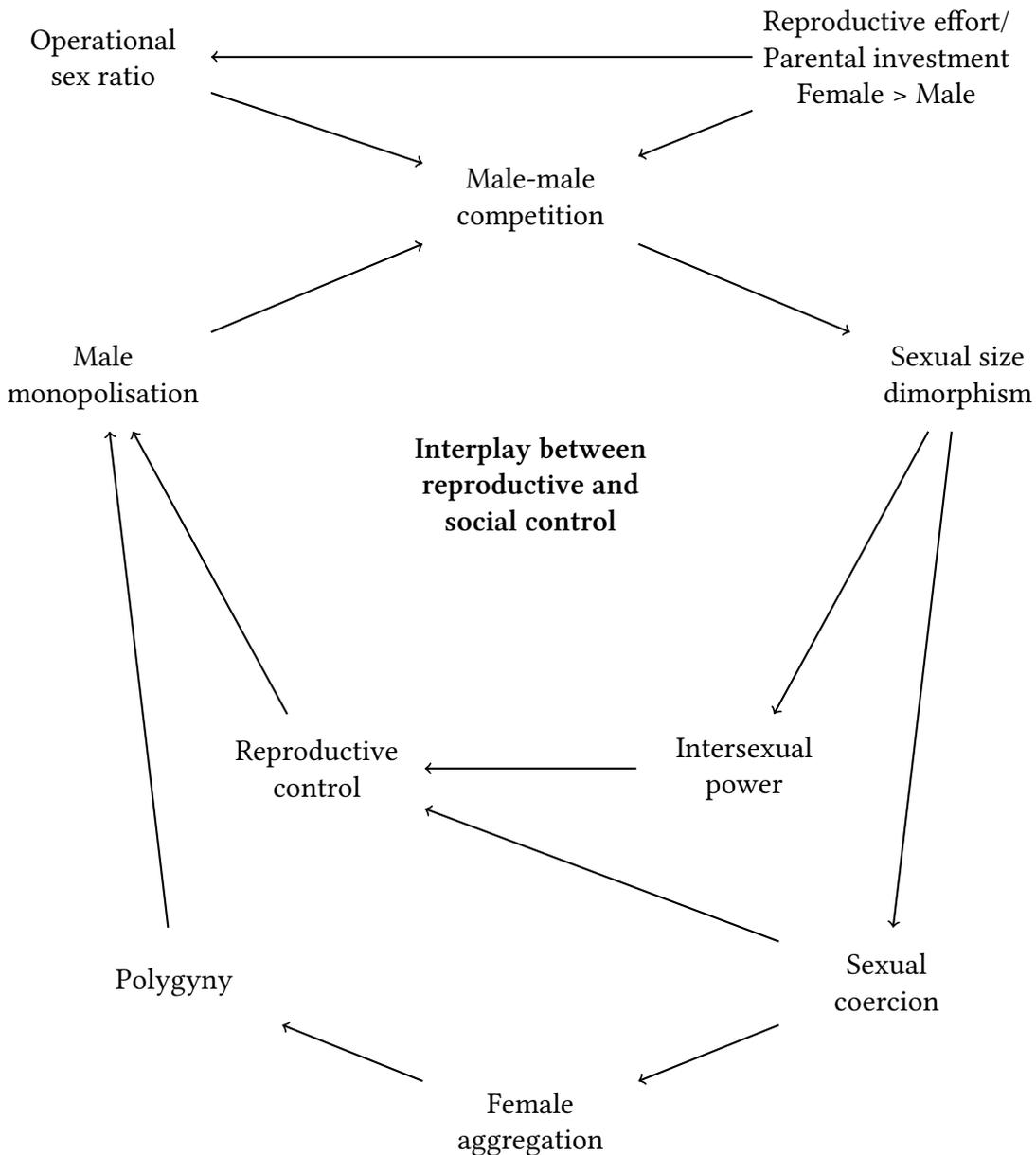


Figure 5: Postulated sequence of evolutionary events. Initially sexual selection operates on male intrasexual competition resulting in the evolution of male-biased sexual size dimorphism which facilitates sexual coercion and male-biased power. Both male power and coercion reduce female reproductive control while females aggregate in order to avoid male coercion giving rise to the evolution of polygyny. Finally, polygyny and reduced female reproductive control facilitate male monopolisation that reinforces male-male competition.

females are expected, in general, to disrupt this loop in order to increase their latitude to express mate choice.

Sexual coercion constrains female mate choice

Female mate choice strategies are well documented in primates and other mammals. Females often have a “*tendency toward active promiscuity*”, they can transfer between social groups or influence the composition of their own (Kappeler and Schaik, 2004). Even in pair-living species, which are supposed to exhibit the highest level of monandry, females may initiate extra-pair copulation (Kappeler and Schaik, 2004). The increased body of evidence regarding the expression of male sexual coercion (Muller and Wrangham, 2009; Wallen et al., 2016; Baniel, Cowlshaw, and Huchard, 2017), however, highlights the caution needed when interpreting certain female behaviours that are traditionally considered as expression of mate choice. Previous studies have suggested that female strategies such as female copulation solicitations to multiple males and promiscuous mating aim to improve female reproductive success by confusing paternity and decreasing infanticide risk (Lukas and Huchard, 2014) or by increasing fertilization probability and/ or offspring genetic quality through sperm competition (Simmons, 2005; Fisher et al., 2006). Observations of female avoidance or approach of certain males has been used to quantify female mate preferences, because proximity patterns of heterosexual dyads appear to influence mating outcomes. Female yellow baboons (*Papio cynocephalus*) for example, can actively maintain proximity and influence consortship duration with particular males that is positively associated to male mating success (Bercovitch, 1995). Such female behaviours and mating patterns may seem to result indeed from female mate choice, but they may be imposed by social constraints (intra- or intersexual conflicts) and in particular male sexual coercion (Clutton-Brock and McAuliffe, 2009). Therefore, females in species where males use sexual coercion, may approach, solicit or mate with several males in order to reduce the coercion they receive from them (Smuts and Smuts, 1993; Huchard et al., 2012). This hypothesis is also supported by the observation of females who both mate promiscuously and try to avoid males, like female thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*; Schwagmeyer, 1984).

Observations and previous studies in mandrills suggest that females may express mate choice. First, female mandrills can interrupt copulation before male ejaculation and escape males running up in trees (personal observation) taking advantage of their small size compared to males and the dense vegetation characterizing their natural habitat. Second, high-ranking females can outrank certain males (*Chapter 1*) and thus, they may indicate that these females may have, at least to some extent, the latitude to express mate choice when it comes to these males they outrank. Third, female mandrills might hold some extent of 'social power' and through affiliation with males can influence male dominance status (*Chapter 1*) which is strongly associated to the reproductive outcomes (Charpentier et al., 2020; Charpentier et al., 2005). Fourth, alpha male mandrills do not sire about one third of offspring born during a birth cohort (Charpentier et al., 2005; Charpentier et al., 2020), meaning likely that a large percentage of females are not coerced to reproduce with him and they might be able to choose their mates. Finally, a previous study of a mandrill population under semi-free conditions suggests that female mandrills exhibit female mate choice - indexed by proximity rates and acceptance of male approaches or sexual inspections - and they prefer brightly coloured males (Setchell, 2005). Nevertheless, the results presented in *Chapter 2* underlining the expression of sexual coercion from male mandrills, as suggested above, may cast doubts on the reproductive control of females. Alpha male mandrills monopolise the majority of periovulatory mate guarding (which is a good predictor of paternity; Setchell, Charpentier, and Wickings, 2005a) while they copulate (*Chapter 2*) and reproduce more than all other males (Charpentier et al., 2020; Charpentier et al., 2005). However, other males are also coercive and female mate choice might be constrained by them as well. Hence, the observed female mandrill behaviours of escaping male mating attempts or interrupting copulation may aim to reduce the probability of receiving male sexual aggression or punishment by other coercive males in proximity rather than reflecting the expression of mate choice.

Why are male mandrills purple-buttred then?

In mandrills, males are strikingly more colourful - in face, rump and genitalia - than females (Setchell and Dixson, 2001a; Setchell, 2005) and their colouration has attracted attention since the conception of the theory of sexual selection as a trait potentially at-

tractive to females (Darwin, 1871). In birds, male ornaments often communicate male qualities that can be, indeed, used as cues chosen by females (Devlin Calkins and Tyler Burley, 2003; Pradhan and Schaik, 2009) and can be correlated to different physiological or behavioural male characteristics. In Northern Cardinals (*Cardinalis cardinalis*), for example, male colour is correlated to body size and condition as well as to the levels of paternal care and reproductive success (Jawor and Breitwisch, 2004). However, ornaments may serve different purposes apart from mate choice.

The costs of physical fights among competitive individuals may lead to the evolution of traits and signals that can assist in conflict management and reduce aggression rates (Preuschoft and van Schaik, 2000). Competitors may use such signals to infer the competing abilities of each other and weak or subordinate individuals may submit to stronger or dominant individuals without retaliating in order to avoid the costs of fights that are most likely going to lose; accordingly, the risk of escalation might be greater when power asymmetries between the competing individuals seem to be low, because the outcome of a fight is imponderable (Clutton-Brock et al., 1979; Drews, 1993; Gordon and Lea, 2016). In mandrills, the extreme armaments of males including ~4.5cm long canines (Leigh et al., 2008) likely render physical fights very costly. Indeed, such fights may lead to severe injuries or even death (Setchell and Jean Wickings, 2005). In addition, the colouration of male mandrills is correlated with dominance rank (Setchell and Dixson, 2001b; Setchell et al., 2008; Renoult et al., 2011) and can reflect testosterone levels (Dixson, Bossi, and Wickings, 1993; Setchell and Dixson, 2001b) or competitive ability and willingness to engage in fights (Setchell et al., 2008). Hence, male mandrill colouration may act as a 'badge of status' (Setchell and Jean Wickings, 2005; Setchell et al., 2008) that can minimize superfluous physical fights and render a 'colour contest' sufficient to resolve most conflicts. A number of observations supports this hypothesis. First, fights among male mandrills are rare (Setchell and Jean Wickings, 2005). Second, fights occur mostly among similarly coloured males, while submission occurs mostly among males with larger colour differences (Setchell and Jean Wickings, 2005). Finally, the highest-ranking male exhibits the brightest and most extensive colouration (Setchell and Jean Wickings, 2005) which usually decreases when he loses his dominant position (Setchell and Dixson, 2001b). It is worth noting that in an exceptional case, when an alpha male lost its rank but maintained its colouration, female behaviours towards him did not change but he stopped

mating (Setchell, 2005). This suggests that female mandrills may show indeed a preference for colourful males, but if this is not reflected on the mating, and most importantly, on the reproductive outcomes then female choice - *sensu stricto* - may not function.

The drivers of female sexual behaviour are thus often hard to interpret. A female may mate, solicit, approach or avoid a male either to express mate choice or to avoid sexual coercion, while both female choice and male coercion may co-occur (as in chimpanzees: Muller et al., 2007; Watts, 2022; Pieta, 2008; Kaburu and Newton-Fisher, 2015; see introduction) making their untangling a complicated task. Indeed, a combination of results from a handful of studies suggests that male sexual coercion may not necessarily rule out the expression of female mate choice. In mosquitofishes (*Gambusia holbrooki*), for example, when females are deprived of males, they express mate choice exhibiting an increased rate of approach and decreased rate of avoidance of males, while they are more coerced by males than non-deprived females (Bisazza, Vaccari, and Pilastro, 2001). Moreover, in humans vast evidence underline that women can express mate choice (Puts, 2010) but sexual coercion is also frequently observed (Basile, 2002). In conclusion, the results of *Chapter 2* on sexual coercion and the high reproductive skew in favour of alpha male mandrills suggest that male-male competition may exercise a stronger selective pressure than female choice on their current reproductive outcomes, but female mandrills might still be able to exert mate choice.

How can females express mate choice when they are sexually coerced?

Females may be able to bypass the reproductive costs of sexual coercion and they may express mate choice thanks to a combination of certain behavioural and physiological adaptations. Behavioural strategies include the distraction of males in order to escape male monopolisation and mate guarding. For example, female banded mongooses (*Mungos mungo*) can incite conflicts between their group and neighboring ones, during which they mate with extra-group males (Johnstone et al., 2020). Also, females may influence the identity of the males who are coercing them and with whom they have a highest probability to mate. In particular, females may promote male-male competition and influence male dominance status which is highly related to reproductive success (Keller

and Reeve, 1994; Setchell and Jean Wickings, 2006; Charpentier et al., 2020) and potentially to coercion potential as well (*Chapter 2*). Copulation calls (African elephants (*Loxodonta africana*): Poole, 1989; Barbary macaques (*Macaca sylvanus*): Semple and McComb, 2000) or prolonged sexually receptive periods as well as mating signals such as sexual swellings (Zinner et al., 2004) that advertise female receptivity or attract males may promote male-male competition (including sperm competition; Cox and Le Boeuf, 1977; Poole, 1989; Domb and Pagel, 2001; Zinner et al., 2004). Female mandrills exhibit sexual swellings (Setchell, 2004) and they may also influence male dominance rank through their social bonds with them (*Chapter 1*). Given that females appear to receive significantly more coercion from the highest-ranking males (*Chapter 2*), they can potentially indirectly ‘choose’ the male from whom they receive the most coercion and with whom they appear to have increased probability to mate (*Chapter 2*).

Females can display unreliable signals of ovulation to deceive males and mate outside of oestrus, like in bonobos (Douglas et al., 2016), vervet monkeys (Andelman, 1987) or hamadryas baboons who are also sexually coercive (Zinner and Deschner, 2000; Swedell and Schreier, 2009). Females may also use postcopulatory mate choice. In a number of bat species, females can increase their reproductive control through cryptic female choice, i.e. by discarding sperm of unwanted males and thus, biasing the fertilization success (Birkhead and Pizzari, 2002). Such strategies, however, require that female promiscuity is not constrained by males, so a female can choose among the sperm of different males. Females mandrills are often observed to sneakily copulate with males other than the one which is mate guarding them, facilitated by the dense vegetation in their habitat (Setchell and Kappeler, 2003). In addition, similarly to other primates (Gust, 1994), female mandrills often dart (jump or run away) at the end of a copulation. This darting behaviour might constitute another adaptation increasing the control over fertilization probability, given that male sperm may end up outside a female’s vagina (personal observation).

Finally, females may profit of their social environment. In pinnipeds, male coercion may constitute a selective pressure for the evolution of reproductive aggregation. Individual females may receive less male harassment when they breed in large groups (e.g. in American sea lions (*Otaria flavescens*): Cappelzozzo, Túnez, and Cassini, 2008) or when they show higher levels of reproductive synchrony (e.g. in grey seals (*Halichoerus grypus*): Boness,

Bowen, and Iverson, 1995). Mandrills live in groups that count hundreds of individuals (Abernethy, White, and Wickings, 2002) where the sex ratio is strongly female biased (Hongo et al., 2016). They reproduce seasonally (most conceptions occur between June and August: Dezeure, Charpentier, and Huchard, 2022) and each female oestrous cycle lasts for several days. As a consequence, females often show overlapping cycles (Setchell and Wickings, 2004) and a given male may fail to monopolise mating access to multiple simultaneously receptive females (Charpentier et al., 2005), similarly to other primates characterized by reproductive synchrony (Ostner, Nunn, and Schülke, 2008). Hence, simultaneously cycling female mandrills may manage to express mate choice bypassing alpha male monopolisation.

Can females use social strategies to mitigate sexual coercion?

The present work examined if, in order to express mate choice and/or mitigate the effect of male sexual coercion, female mandrills use social strategies. In particular the potential protective value of social bonds with a particular male, all males or other females was examined. Social bonds constitute indeed a crucial factor for the expression of sexual coercion in mandrills (*Chapter 3*) similarly to other species (Clarke et al., 2009; Kunz et al., 2021b), but contrary to predictions, the results of this work suggest that social bonding is positively correlated to sexual coercion: more bonded females with particular males, all males or female groupmates, receive more male coercion than less bonded females.

Female-male bonds. Female mandrills who form stronger affiliative relationships with particular males appear to receive more coercion from these males. This result suggests that in species where males use sexual coercion as a mating strategy, females may receive coercion even from their male partners but the causality of this relationship is not clear yet. On the one hand, the observed association patterns of females with particular males might be a result of coercion. In hamadryas baboons (*Papio hamadryas hamadryas*), males use coercion against their female partners, potentially to force them stay close and reduce the chances that they will mate with rival males (Swedell and Schreier, 2009). Accordingly, in bottlenose dolphins (*Tursiops aduncus*), males aggressively enforce proximity with females (King et al., 2019). Hence males may coerce females into associa-

tions. On the other hand, female-male associations may be characterized de facto by high levels of male coercion because coercive males assault more the females close to them. Nonetheless, a number of empirical evidence is at odds with this last hypothesis. First, in chacma baboons, where males use sexual intimidation against females similarly to mandrills (Baniel, Cowlshaw, and Huchard, 2017), females form associations with particular males which are characterized by high levels of proximity but low levels of aggression (Palombit, Seyfarth, and Cheney, 1997; Baniel, Cowlshaw, and Huchard, 2016). Second, animal groups are often highly structured and the social environment of an individual is unlikely to be random, but instead it reflects the existence of differentiated relationships between group members (Lusseau, 2003; Croft et al., 2005). Therefore, the increased coercion that female mandrills receive from males with whom they maintain stronger affiliative bonds (*Chapter 3*) is unlikely to result exclusively from the incidental spatial proximity of the dyad members.

Similarly to hamadryas baboons (Swedell and Schreier, 2009), male mandrills may use coercion to increase their control over the movement and reproductive activity of their female partners. Alternatively, males may assault their partners when other males are in proximity in order to advertise their vigor and strength to these rivals or in order to protect their bond with the female. Chimpanzees may react agonistically towards interacting dyads when they have a strong affiliative bond with one of the dyad members (Webb et al., 2020) while in humans where intimate partner violence and sexual coercion are widespread (Basile, 2002), male sexual jealousy represents the most common cause for wife beating (Smuts, 1992). Similar functions of ‘jealousy’, i.e. to retain a valuable social bond against potential intruders (Hart and Legerstee, 2010) have been documented in other mammals across different contexts (i.e. not only sexual; Tutin, 1979; Webb et al., 2020; Harris and Prouvost, 2014) and may resemble the behaviour of male mandrills, when their bond is threatened by rival males.

In species where females form highly differentiated affiliative bonds with particular males, males may protect the infants of their female partners from attacks of other males (Palombit, 1999) while in other species intersexual bonds may also protect females from male harassment (Fox, 2002). However, female mandrills do not appear to form highly differentiated bonds with particular males (*Chapter 3*) and when they form stronger bonds

with their top male partner do not receive less coercion from all other males, i.e. their male partners do not protect them against coercion (*Chapter 3*). Certain characteristics of mandrills may explain why they do not form such differentiated intersexual bonds.

In order to protect their female partners, male mandrills would likely have to encounter the alpha male who is the one directing the most sexual coercing to females (*Chapter 2*). However, encountering the alpha male may constitute a high risk for most males and their bonds with their female partners may not offer sufficient (long-term) benefits that can counterbalance such risks. This argument may seem at odds with the differentiated intersexual bonds in baboons (Smuts, 1985; Palombit, Seyfarth, and Cheney, 1997; Baniel, Cowlshaw, and Huchard, 2016) who are also sexually coercive (Swedell and Schreier, 2009; Baniel, Cowlshaw, and Huchard, 2017). However, baboons typically breed year-round (Swedell, 2010) and intersexual bonds may serve as paternal care (Buchan et al., 2003; Baniel, Cowlshaw, and Huchard, 2016). Conversely, female-male relationships in mandrills last usually for a limited time period because most males usually emigrate after the mating season (Brockmeyer et al., 2015) and the ‘mate-then-care’ hypothesis has few empirical support in this species.

Unexpectedly, the strength of a female’s bond with her top male partner appeared positively correlated to the coercion rate she receives from all other males (*Chapter 3*), suggesting that bonds with particular males may render females vulnerable to aggression by other males. In other species, high-ranking males may attack the female partners of low-ranking males, presumably to provoke aggressive confrontations that they are likely to win (Smuts, 1985). In addition, by assaulting females who preferentially maintain proximity to low-ranking males, high-ranking males may disrupt this proximity ‘bond’ of the female with rival males and prevent females from expressing mate choice (Manson, 1991). Hence, the increased male mandrill aggression towards females which form stronger bonds with particular males may reflect an effect of male-male competition where males aim to ‘steal’ the female partner of a rival male or to intimidate her in order to decrease her mating rate with her partner, in a form of sexual coercion in-between intimidation and punishment.

Female-female bonds. In species that live in polygynandrous groups and where the members of one sex disperse (like male mandrills), intersexual social bonds may be more

transient than intrasexual bonds. Based on this hypothesis, the effect of bonds among philopatric female mandrills on sexual coercion was also examined. Surprisingly, female mandrills appeared to receive more male coercion when they were more bonded to their female groupmates (*Chapter 3*). This effect is opposite to previous studies showing, for example, that higher social integration of female feral horses may reduce harassment by males (Cameron, Setsaas, and Linklater, 2009). These results add to a handful of recent studies which suggest that social bonding can be associated with certain costs. In prairie voles (*Microtus ochrogaster*), individuals with an intermediate (vs high) number of social bonds exhibit higher fitness (Sabol et al., 2020). Also, female eastern grey kangaroos (*Macropus giganteus*) with bigger social networks or higher numbers of bonds with other females exhibit reduced offspring survival rates (Menz et al., 2020). Finally, yellow-bellied marmots (*Marmota flaviventris*; Blumstein et al., 2018) and blue¹ monkeys (*Cercopithecus mitis stuhlmanni*; Thompson and Cords, 2018) experience trade-offs between their social bonds and their longevity. The results in *Chapter 3* are not sufficient, however, to suggest that social bonds are associated with fitness costs for female mandrills since male coercion probably does not counterbalance the benefits of social bonding. In fact, a large number of studies suggests that social bonds offer important fitness benefits to bonded individuals (see introduction) and more bonded female mandrills also appear to enjoy higher reproductive success (Charpentier et al., 2012). Nonetheless, a question remains: why do more bonded females receive more male coercion?

First, in several species, including some where males are sexually coercive, males prefer to reproduce with females that have high reproductive success. For example, male chimpanzees are sexually coercive (Muller et al., 2007) and mate preferentially with older females (Muller, Thompson, and Wrangham, 2006) who have higher reproductive success (Pusey, Williams, and Goodall, 1997) than younger females. Similarly, male mandrills may also prefer mating with high-ranking and parous females which produce offspring of higher quality than low-ranking or nuliparous females (Setchell and Jean Wickings, 2006). Therefore, more bonded females, which often have higher reproductive success (Charpentier et al., 2012), may receive more male coercion because coercive males prefer these females as mates ('attractiveness hypothesis'). Second, dominant individuals are often more aggressive than subordinates (Jackson, 1988). In addition, relatively recent

¹

evidence in humans suggests that the risk of retaliation is often greater when the competing individuals are of similar dominance rank (Gordon and Lea, 2016) and accordingly more powerful women who may receive more sexual harassment may also respond to male sexual harassment more assertively (Gruber and Bjorn, 1986; Folke et al., 2020). Therefore, more bonded female mandrills, which might possess higher dominance rank and likely enjoy higher social support, may receive more male coercion because they are more reluctant to comply to male mating strategies and males need to assault such females more in order to make them comply to their will ('retaliation hypothesis').

The results in *Chapter 3* did not support neither the 'attractiveness' nor the 'retaliation hypothesis', i.e. the positive correlation of female-female bonds with male coercion a female mandrill receives, appears independent of female reproductive success and dominance rank. However, the results of different analyses (*Chapter 2 & 3*) suggest that high-ranking females in general receive more male coercion than low-ranking females. The combination of these results indicate that the costs (or benefits) of social bonds can be independent of dominance rank (for an example of independent benefits see: Silk, Alberts, and Altmann, 2003) despite the correlation of dominance and bonding in several species (Vulllioud et al., 2019; Wooddell, Kaburu, and Dettmer, 2020). A potential explanation for such phenomenon is that in large animal groups, like mandrill groups, females may have the latitude to form multiple and/or strong social bonds with groupmates regardless of their rank.

Social bonds appear to have a rather direct effect on coercion supporting the 'public exposure hypothesis'. Namely, more bonded females may receive more male coercion because they interact more with their groupmates than peripheral females and thus, they may also interact more with coercive males who coerce them more. This hypothesis may also be supported by the results of *Chapter 3* as a whole which suggest that females which are overall more bonded (with males or females) receive more male coercion. Alternatively, the increased coercion towards more bonded females may reflect other pathways which are not obvious and female reproductive success or dominance rank may still play some role but with an intensity below the ability of the performed analysis to detect it. Altogether, female mandrills seem to experience trade-offs between sexual coercion and the formation of social bonds with their groupmates but it is not clear yet if such trade-offs

translate into fitness costs.

Conclusions and future prospects

The present work describes the social and reproductive struggles between the sexes in a wild promiscuous social primate, the mandrill. These results suggest that females can occasionally dominate males even when they are clearly physically inferior to them. Along with a handful of recent studies, they indicate that future work on dominance dynamics should consider intersexual interactions rather than focusing only in one sex which may offer a limited view on the social landscape of a species. In addition, the expression of sexual intimidation by mandrills reinforces the hypothesis that this coercive male mating strategy which is hard to identify can be widespread in polygynandrous and/ or sexually dimorphic mammals where males are dominant over females, but detailed studies on more species need to confirm or reject this speculation. Finally, female-female bonds seem more influential than intersexual bonds in the social landscape of mandrill groups and further research should quantify the effect of female coalitions on the competition between the sexes for social and reproductive control.

The different forms of sexual coercion seem widespread in mammals including humans (Muller and Wrangham, 2009) and except obvious forms such as infanticide which has long been described as such (Palombit, 2015) - potentially due to striking observations of infant deaths - sexual coercion includes forms harder to observe, like sexual intimidation. As a consequence, studies on female choice which might operate in opposite direction than sexual coercion, may need to control if female behaviours that are often perceived as expression of mate choice are only expressed when females aim to avoid coercion. Similarly, the constraints that sexual coercion impose on female mate choice have to be examined, along with the potential fitness costs (e.g. reduced reproductive success) for females. Additionally, the evolutionary consequences of female empowerment remain unknown in mandrills and an open question remains if more powerful females have more opportunities to express mate choice or they are less vulnerable to sexual coercion.

Finally, the documentation of sexual coercion in one more sexually dimorphic and broadly male dominant species suggests that male-biased intersexual power asymmetries may

promote both male dominance and sexual coercion, as already speculated. Studies on sexual selection may consider intersexual dominance dynamics and sexual coercion part of the same feedback loop (Figure 5) that determines the control that each sex has over reproduction, the determining resource in the operation of natural and sexual selection.

French summary

Résumé

Les conflits socio-sexuels entre les sexes peuvent façonner les systèmes sociaux et reproducteurs chez de nombreuses espèces animales. L'asymétrie de pouvoir entre les sexes, souvent liée à un fort dimorphisme sexuel en faveur des mâles, permet souvent aux mâles de dominer socialement les femelles et d'utiliser des stratégies sexuelles coercitives pour leur imposer leurs choix. Cependant, les femelles peuvent résister aux stratégies des mâles par des adaptations comportementales, comme en sollicitant l'aide de partenaires sociaux. De telles stratégies femelles pourraient être répandues, mais leur étude exige une collecte systématique de données sur de longues périodes. Cette thèse examine la nature des relations socio-sexuelles chez les femelles et les mâles mandrills (*Mandrillus sphinx*), grâce à une base de données de long-terme. Les mandrills sont des primates d'Afrique Centrale vivant dans de grands groupes polygynandres et présentant un dimorphisme de taille extrêmement biaisé en faveur des mâles. Pourtant, les femelles, qui sont philopatriques chez cette espèce, montrent des relations sociales hautement différenciées et forment parfois des coalitions contre les mâles migrants dans leur groupe. Ainsi, l'étude des conflits socio-sexuels entre les sexes et de l'influence du paysage social sur ces conflits apparaît très pertinente chez cette espèce. Le premier chapitre étudie la dynamique de dominance entre les sexes (*Chapitre 1*). De récentes études ont dessiné un paysage dynamique avec plusieurs facteurs influençant les relations de dominance entre les sexes, tandis que la compréhension des processus évolutifs favorisant la dominance d'un sexe sur l'autre reste fragmentaire. Les mandrills femelles dominant, en moyenne, 11% des mâles adultes, tandis que la hiérarchie intersexuelle constitue, elle, une inter-

digitation des hiérarchies intrasexuelles mâles et femelles. De plus, l'intégration sociale dans le réseau des femelles favorise le statut de dominance des deux sexes: les individus les mieux intégrés socialement ont un statut de dominance plus élevé. Les deux autres chapitres étudient l'expression et la nature de la coercition sexuelle (*Chapitre 2*) et l'effet de l'intégration sociale d'une femelle sur la coercition qu'elle subit de la part des mâles (*Chapitre ??*). Les mandrills mâles semblent utiliser une forme de coercition sexuelle consistant à agresser les femelles de façon répétée, parfois longtemps avant leur période de fertilité, afin d'améliorer leur succès d'accouplement à long terme, à savoir de l'intimidation sexuelle. L'intimidation sexuelle n'a été montrée auparavant que chez deux autres espèces de primates, mais ces résultats suggèrent que cette stratégie pourrait être répandue chez les mammifères sexuellement dimorphiques et vivant en grands groupes multimâles-multifemelles. Par ailleurs, les femelles de rang supérieur et les plus intégrées socialement (avec des mâles ou d'autres femelles) semblent recevoir plus de coercition de la part des mâles, principalement de la part de leurs partenaires sexuels et des mâles de haut rang. Ce travail montre que les mâles et les femelles peuvent varier dans leurs propensions à utiliser ou à recevoir la coercition sexuelle, respectivement, et les femelles semblent faire l'expérience de compromis entre leurs relations d'affiliation et la coercition sexuelle qu'elles subissent de la part des mâles. De manière générale, les relations intersexuelles semblent représenter une course aux armements entre les sexes pour, entre autres, le contrôle de la reproduction, une ressource déterminante dans le fonctionnement de la sélection naturelle (et sexuelle).

Introduction

Dominance intersexuelle

La dominance intersexuelle, à savoir les relations de dominance sociale entre les individus de sexe opposé et qui se construit sur le pouvoir basé sur la force ou la possibilité d'utiliser la force d'un sexe sur l'autre (Lewis, 2002; Lewis, 2018), a longtemps été polarisée en deux catégories, à savoir les espèces chez qui les mâles sont socialement dominants sur toutes les femelles et son contraire. Cependant, des études récentes qui

ont quantifié la dominance intersexuelle via la construction de hiérarchies intersexuelles mesurant le biais lié au sexe dans l'issue des conflits intersexuels, dessinent un paysage plus nuancé et dynamique (Lewis, 2020; Davidian et al., 2022; Kappeler et al., in press). La dominance intersexuelle varie le long d'un continuum, comprenant des relations de dominance mâle-femelle plus équilibrées (par exemple: Hemelrijk et al., 2020). Toutefois, notre compréhension des raisons pour lesquelles la dominance intersexuelle peut être biaisée envers les femelles chez certaines espèces, et envers les mâles chez d'autres, reste fragmentaire et repose souvent sur des hypothèses spécifiques au taxon étudié (Lewis, 2018; Kappeler and Fichtel, 2015; Davidian et al., 2022).

Outre les différences physiques entre les sexes (taille ou force musculaire) ou comportementales (agressivité), d'autres facteurs peuvent influencer l'issue des conflits intersexuels (Lewis, 2002; Davidian et al., 2022). Ces facteurs comprennent: (i) l'état reproducteur, les femelles dominant une plus grande proportion de mâles quand elles sont sexuellement réceptives (Smith, 1980), (ii) le sex-ratio du groupe, les femelles dominant une plus grande proportion de mâles quand le nombre de mâles dans le groupe augmente (Lewis, 2020; Izar et al., 2021; Hemelrijk et al., 2020) ou encore (iii) les alliances sociales entre femelles et/ou avec des individus dominants (Bissonnette, de Vries, and van Schaik, 2009; Vulllioud et al., 2019; Strauss and Holekamp, 2019).

Coercition sexuelle

Bien que les relations de dominance représentent une part non-négligeable des interactions intersexuelles, ces interactions ont très souvent lieu dans un contexte sexuel. Les intérêts évolutifs divergents des mâles et des femelles conduisent souvent à des conflits sexuels. Alors que le succès reproducteur des femelles est généralement limité par les coûts élevés de la reproduction, tels que la gestation et la lactation chez les mammifères, le succès reproducteur des mâles est principalement déterminé par le nombre de partenaires d'accouplement (Bateman, 1948). Chez certaines espèces, les mâles utilisent la coercition sexuelle envers les femelles, définie comme 'l'utilisation par un mâle de la force, ou de la menace de la force, pour augmenter les chances qu'une femelle s'accouple avec lui à un moment où elle est susceptible d'être fertile, ou pour diminuer les chances

qu'elle s'accouple avec d'autres mâles, entraînant un coût pour la femelle' (Smuts and Smuts, 1993; Clutton-Brock and Parker, 1995b).

Les écologues du comportement ont traditionnellement documenté des stratégies coercitives qui sont immédiatement visibles, telles que la copulation forcée (lorsqu'une femelle est physiquement restrainte par un mâle pour s'accoupler avec lui) et le harcèlement sexuel (lorsque l'agression précède immédiatement la copulation et est dirigée contre la femelle jusqu'à ce qu'elle cède; Smuts and Smuts, 1993). En revanche, les formes de coercition sexuelle qui fonctionnent sur le long terme - lorsque l'agression ne se traduit pas immédiatement en avantages reproducteurs pour l'agresseur mais plus tard - sont plus difficiles à mettre en évidence, et ont été moins étudiées en dehors des sociétés humaines (Muller and Wrangham, 2009). Par exemple, l'intimidation sexuelle, lorsque l'agression répétée des mâles sur une période prolongée vise à forcer les femelles à accepter de s'accoupler avec eux lorsqu'elles deviennent fertiles, n'a jusqu'à présent été documentée que dans deux sociétés de primates (chimpanzés (*Pan troglodytes*): Muller et al., 2007; babouins chacma (*Papio ursinus*): Baniel, Cowlishaw, and Huchard, 2017). Les mâles de différents taxons (par exemple les oiseaux et les primates, y compris les humains) peuvent également punir les femelles à la suite de copulations avec des mâles rivaux pour décourager de tels comportements dans le futur (Clutton-Brock and Parker, 1995a; Valera, Hoi, and Krištín, 2003; le Roux et al., 2013; Rodseth and Novak, 2009). Ces comportements punitifs sont également peu reportés dans le règne animal.

Liens sociaux et coercition sexuelle

Des études récentes se sont concentrées sur les avantages pour les mâles sexuellement coercitifs mais on en sait beaucoup moins sur la façon dont les femelles peuvent minimiser la coercition qu'elles reçoivent ou comment elles peuvent équilibrer ces rapports de force. Chez les espèces sociales, les femelles peuvent utiliser leurs relations sociales pour prévenir ou résister à l'agression des mâles. Par exemple, les pinnipèdes femelles peuvent se reproduire en grands groupes pour diluer le risque d'agression de la part des mâles (Cappozzo, Túnez, and Cassini, 2008) tandis que les femelles primates peuvent former des associations mâle-femelle à long terme pour minimiser le risque d'infanticide

(Van Schaik and Kappeler, 1997; Palombit, 1999) ou d'agression par les conspécifiques (Nguyen et al., 2009). Les femelles qui forment des relations d'affiliation plus fortes avec certains mâles peuvent être moins agressées par ces mâles (Haunhorst et al., 2017), tandis que, plus généralement, les liens sociaux intersexuels peuvent apporter d'autres bénéfices aux femelles en terme de fitness (Archie et al., 2014). Par ailleurs, l'intégration sociale des femelles avec d'autres femelles peut réduire le harcèlement par les mâles (chez les chevaux sauvages: Cameron, Setsaas, and Linklater, 2009). Les agresseurs potentiels peuvent, en effet, hésiter à agresser les femelles bien intégrées socialement et pouvant potentiellement former des coalitions entre elles et exercer des représailles contre eux (Bro-Jørgensen, 2011; Smuts and Smuts, 1993). Alors qu'une connectivité élevée d'un individu avec ses conspécifiques par le biais de liens affiliatifs peut lui offrir de multiples avantages tels qu'une réduction du stress ou du risque de mortalité (humains: House, Landis, and Umberson, 1988; Seeman et al., 2002, une telle connectivité pourrait avoir un impact supplémentaire sur la coercition sexuelle, en la diminuant.

Objectifs

L'objectif central de cette thèse est d'explorer les conflits sociaux et reproductifs entre les mâles et les femelles chez les mandrills. Le premier chapitre décrit les relations de dominance entre les femelles et les mâles adultes. Il vise à clarifier si les femelles peuvent dominer socialement certains mâles et les facteurs qui peuvent influencer ce phénomène, avec un accent particulier sur l'effet des liens sociaux entre femelles et mâles, ainsi qu'entre femelles. Le deuxième chapitre examine si les mâles mandrills utilisent la coercition sexuelle contre les femelles afin d'obtenir des opportunités d'accouplement, tout en clarifiant le mécanisme par lequel la coercition sexuelle s'opère. En particulier, les trois prédictions de la coercition sexuelle sont testées (Smuts and Smuts, 1993), à savoir si l'agression des mâles (i) cible davantage les femelles sexuellement réceptives que les femelles dans d'autres états reproducteurs, (ii) est coûteuse pour les femelles sous la forme d'une plus grande exposition aux blessures, et (iii) augmente le succès de l'accouplement du mâle avec sa victime. Le troisième chapitre se concentre sur les effets des liens sociaux et génétiques des femelles sur la coercition sexuelle qu'elles reçoivent, dans le but de

clarifier si les femelles mieux intégrées socialement reçoivent plus ou moins de coercition de la part des mâles que les femelles moins intégrées socialement. Enfin, ce dernier chapitre cherche à comprendre comment le rang de dominance et le succès reproducteur des femelles modulent l'influence des liens sociaux sur la coercition sexuelle.

Modèle d'étude

Les primates constituent un bon modèle biologique pour étudier la dominance intersexuelle et les conflits sexuels car la diversité de leurs systèmes sociaux et d'accouplement peut favoriser diverses stratégies sexuelles mâles et femelles, tandis que leurs capacités cognitives souvent développées, notamment la mémoire à long terme des interactions sociales, peuvent faciliter l'utilisation de stratégies sociales et reproductives fonctionnant sur le long terme (Stumpf et al., 2011). De telles stratégies devraient également être favorisées par le fait que de nombreux primates vivent dans des groupes bisexuels stables où mâles et femelles entretiennent des relations socio-sexuelles différenciées, et sont caractérisés par un dimorphisme sexuel fréquemment biaisé en faveur des mâles, associé à des systèmes d'accouplement polygynes ou polygynandres.

Chez les mandrills, un primate de la famille des *Cercopithecidae*, les accouplements semblent largement contrôlés par les mâles (Charpentier et al., 2005) bien que les femelles semblent pouvoir exercer un certain niveau de choix de partenaire en contrant les stratégies des mâles (Setchell, 2016). Les mandrills se reproduisent de manière saisonnière et vivent en groupes polygynandres où les femelles sont philopatriques et les mâles immigrent au début de la saison des accouplements (Brockmeyer et al., 2015). Ce séjour temporaire des mâles dans le groupe les rend probablement moins intégrés socialement que les femelles. Les mâles se livrent à une compétition reproductive intense pendant la saison de reproduction et les mâles de haut rang s'accouplent en priorité avec les femelles réceptives qui présentent des tumescences sexuelles périnéales autour de l'ovulation (Setchell, Charpentier, and Wickings, 2005a). Le dimorphisme sexuel est extrême chez cette espèce (les mâles sont 3,4 fois plus lourds que les femelles; Setchell et al., 2001), mettant en évidence une importante asymétrie de force physique entre les sexes qui peut faciliter l'expression de stratégies coercitives par les mâles. De plus, des observations

ponctuelles de représailles de la part des femelles et de coalitions de femelles contre des mâles (Setchell, Knapp, and Wickings, 2006) soulignent l'effet possible du soutien social des femelles sur les rapports de dominance entre les sexes chez cette espèce.

Ce travail a été réalisé grâce à des données comportementales de long-terme issues du projet *Mandrillus* qui étudie les traits d'histoire de vie, l'écologie et les comportements d'un groupe de mandrills sauvages vivant dans le sud du Gabon.

Résultats

Les résultats de ces travaux sont présentés sous forme de trois manuscrits; le 1er chapitre est en cours d'évaluation d'une revue scientifique, le second a été publié le 20/06/2022 (Smit et al., 2022) et le troisième est en préparation.

Chapitre 1: Dynamique de la dominance intersexuelle chez un primate hautement dimorphe

Un ensemble de données comportementales sur une période de 8 ans a été utilisé pour examiner la dynamique de la dominance intersexuelle chez les mandrills (*Mandrillus sphinx*). La hiérarchie de dominance intersexuelle a été établie sur des blocs consécutifs de 6 mois (représentant les saisons d'accouplement ou de naissance) et a révélé qu'en moyenne, une femelle adulte domine 11% des mâles adultes ou subadultes.

La probabilité pour une femelle de dominer un mâle augmente lorsque le nombre de partenaires sociaux femelles de ce mâle diminue (indexé sur les comportements de toilettage) et lorsque le nombre de partenaires de toilettage de cette femelle augmente. De plus, une femelle a une probabilité plus élevée de dominer un mâle pendant la saison des accouplements que pendant la saison des naissances, ou lorsqu'il y a plus de mâles dans le groupe (par rapport aux femelles). Enfin, une femelle a une probabilité plus élevée de dominer les mâles plus jeunes et plus âgés que les mâles dans la force de l'âge.

De même, la probabilité pour une femelle donnée de gagner un conflit contre un mâle

donné est minimale lorsque celui-ci est dans la force de l'âge (par rapport aux mâles plus jeunes et plus âgés). Enfin, une femelle a tendance à gagner plus de conflits intersexuels lorsque la différence de rang social entre les deux membres de la dyade mâle-femelle concernée est plus faible.

Chapitre 2: La coercition sexuelle dans une population naturelle de mandrills

Les trois prédictions de l'hypothèse de la coercition sexuelle ont été étayées par les résultats, à savoir que l'agression des mâles (1) cible spécifiquement les femelles sexuellement réceptives, (2) inflige des coûts à ces femelles et (3) augmente le succès d'accouplement des mâles sur le long terme. Ces résultats restent vrais en considérant uniquement les menaces non physiques ou les agressions plus sévères. Enfin, les femelles de haut rang se sont avérées les plus ciblées par les mâles, probablement en raison de leurs meilleures performances reproductives, tandis que les mâles de haut rang sont les plus coercitifs.

De façon intéressante, les mâles mandrills usent d'une stratégie d'intimidation sexuelle sur le long-terme : le taux d'agression des mâles subit par une femelle pendant la fenêtre de temps précédant sa période de réceptivité sexuelle à partir du début de la saison d'accouplement pour les mâles résidents, ou à partir de la date d'arrivée du mâle dans le groupe pour les mâles migrants) est significativement et positivement corrélé à la probabilité de copulation de la dyade pendant la période de fertilité de la femelle. Au contraire, nous n'avons pas mis en évidence d'effets de l'agression immédiate (c'est-à-dire pendant la période de réceptivité sexuelle) sur la probabilité de copulation des dyades mâles-femelles étudiées.

Enfin, nous avons montré que les mâles alphas étaient significativement plus agressifs (d'un facteur 2 environ) envers les femelles et qu'ils copulaient plus que les mâles subordonnés, quel que soit l'âge du mâle. Tous les mâles sont également plus agressifs lorsqu'il y a plus de femelles fertiles dans le groupe (par rapport au nombre de mâles).

Chapitre 3: Les femelles ayant des liens sociaux forts sont plus exposées à la coercition sexuelle

De façon contre-intuitive, nous montrons dans ce dernier article que les femelles qui entretiennent des liens sociaux étroits avec certains mâles, ainsi que celles qui sont les mieux intégrées dans les réseaux sociaux (avec les mâles ou avec les femelles) subissent plus de coercition sexuelle.

Nous avons d'abord cherché à comprendre quelles dyades hétérosexuelles étaient les plus coercitives. Les taux de toilettage et l'association spatiale sont positivement corrélés à la coercition au niveau dyadique, ce qui signifie que les dyades les plus liées socialement sont également celles qui sont les plus coercitives.

De la même façon, les liens sociaux entre les sexes ne semblent jamais protecteurs pour les femelles. Au contraire, les femelles les mieux intégrées socialement dans les réseaux intersexuels font face à plus de coercition. Tout d'abord, les femelles qui échangent plus de toilettage avec leur principal partenaire social mâle reçoivent plus de coercition de la part des autres mâles. De plus, les femelles qui sont fortement associées spatialement à leur principal partenaire mâle ne subissent pas moins de coercition de la part des autres mâles.

De la même façon, les femelles entretenant des liens de toilettage forts avec tous les mâles, à l'exception de leur principal agresseur mâle, ne reçoivent pas moins de coercition de la part de ce dernier que les femelles moins connectées socialement avec les mâles.

Enfin, les femelles les plus centrales dans les réseaux de toilettage et d'association spatiale des femelles sont également confrontées à plus de coercition sexuelle de la part des mâles. De la même façon, les femelles appartenant à de grandes matrilineées (familles de femelles qui partagent une mère ou une grand-mère commune) ont reçu plus de coercition.

Discussion

Dominance intersexuelle

Le dimorphisme sexuel de taille biaisé en faveur des mâles est généralement associé à une dominance sociale biaisée envers ce sexe (Kappeler, 1993), tandis que la dominance est plus souvent biaisée en faveur des femelles chez les espèces monomorphes (par exemple: Petty and Drea, 2015). Chez les babouins, un groupe taxonomique phylogénétiquement proche des mandrills qui, comme eux, vivent dans de grands groupes polygynandres de type matrilineaire, les mâles adultes dominent la plupart des femelles et peuvent même être strictement dominants sur elles, comme chez les babouins chacma (Kalbitzer et al., 2015). Cela soulève la question de savoir pourquoi les asymétries sexuelles dans la dominance apparaissent moins prononcées chez les mandrills, alors que ces derniers sont plus dimorphiques sexuellement que les babouins et que, comme eux, les mâles usent de coercion envers les femelles pour augmenter leur succès d'accouplement (Baniel, Cowlshaw, and Huchard, 2017; Smit et al., 2022). Contrairement à la plupart des espèces de babouins, les mandrills se reproduisent de façon saisonnière et une grande proportion de mâles ne sont pas des résidents permanents des groupes. La plupart des mâles immigrant dans le groupe en début de saison des accouplements. Les mâles migrants ne sont donc pas complètement intégrés socialement à leur arrivée dans le groupe, et peuvent mettre un certain temps à entrer dans la hiérarchie intersexuelle. En effet, ces nouveaux mâles sont probablement très bas dans la hiérarchie à leur arrivée, comme c'est souvent le cas chez d'autres espèces (Snyder-Mackler et al., 2016). De même, pendant la saison des naissances, les mâles qui restent dans le groupe sont probablement peu enclins à interagir de façon agonistique avec les femelles en l'absence d'enjeux reproductifs. Dans cette optique, plusieurs études indiquent que, chez certains primates sociaux où les mâles ne sont pas des résidents permanents du groupe, comme chez les mandrills, les conflits intersexuels sont rares car les mâles les évitent et les femelles résidentes peuvent ainsi remporter une grande partie de ces conflits (par exemple: *Erythrocebus patas*; Hall, 1966; Goldman and Loy, 1997).

Pourtant, les femelles mandrills sont plus susceptibles de dominer les mâles pendant la saison des accouplements que pendant la saison des naissances. L'immigration saison-

nière des mâles mandrills pendant la saison des accouplements peut expliquer, au moins en partie, la flexibilité de la dominance intersexuelle au fil des saisons. Conformément à cette explication, lorsqu'il y a plus de mâles dans le groupe (par rapport aux femelles), la probabilité pour une femelle de dominer un mâle est plus élevée. Des études récentes sur d'autres primates ont démontré que lorsque la proportion de mâles dans un groupe est plus élevée, les femelles sont dominantes sur une plus fraction de mâles (Hemelrijk, Wantia, and Isler, 2008; Hemelrijk et al., 2020) en raison des 'effets gagnants-perdants' ('winner-loser effects') car certains mâles affaiblis par une compétition intra-sexuelle intense se retrouvent en bas de la hiérarchie. Alternativement ou en plus, il est également possible que les mâles mandrills adoptent des stratégies d'accouplement alternatives, comme chez les damans des rochers (Bar Ziv et al., 2016) où les mâles résidents de haut rang peuvent rivaliser pour s'accoupler avec les femelles fertiles, tandis que les immigrants de rang inférieur peuvent rester plus périphériques et essayer d'obtenir des accouplements 'en cachette'.

Les mâles mandrills semblent toutefois être moins dominants dans la hiérarchie intersexuelle lorsqu'ils ont moins de partenaires femelles de toilettage, c'est-à-dire lorsqu'ils sont plus périphériques ou moins intégrés socialement. Ce résultat peut indiquer que les mâles qui participent activement à la dynamique sociale du groupe montent simultanément dans la hiérarchie, tandis que les femelles dominant souvent les mâles les plus jeunes, les plus âgés ou périphériques qui peuvent manquer de motivation pour déclencher ou gagner des conflits avec des femelles ou des rivaux. Une telle interprétation est renforcée par les résultats présentés montrant que les femelles dominant, ou gagnent plus de conflits contre les mâles jeunes ou âgés que contre les mâles dans la force de l'âge. De même, les jeunes chimpanzés mâles qui sont physiquement et socialement immatures peuvent être incapables de diriger l'agression contre les femelles aussi efficacement que les mâles plus âgés (Reddy and Mitani, 2020). Conformément à ces résultats, les mandrills femelles peuvent occasionnellement former des coalitions agressives contre les mâles ((Setchell, Knapp, and Wickings, 2006), observation personnelle NS), ce qui peut suggérer que de telles coalitions peuvent aider les femelles à dominer les mâles, de la même manière que chez d'autres espèces (hyènes tachetées: Vullioud et al., 2019; bonobos: Parish, De Waal, and Haig, 2000).

Coercition sexuelle

Les résultats présentés révèlent des aspects importants de l'écologie de la coercition sexuelle dans les sociétés des mandrills. Des agressions répétées sur de longues périodes augmentent la probabilité d'accouplement des agresseurs une fois que les femelles deviennent fertiles. L'intimidation sexuelle a déjà été démontrée chez les chimpanzés et les babouins chacma (Muller et al., 2007; Baniel, Cowlshaw, and Huchard, 2017), deux espèces caractérisées par une violence des mâles relativement élevée envers les femelles.

Chez le mandrill, les mâles alphas sont plus agressifs envers les femelles pendant la saison des accouplements et ils copulent beaucoup plus que les mâles subordonnés. Compte tenu du fort biais reproductif en faveur des mâles alphas chez cette espèce (Charpentier et al., 2020; Charpentier et al., 2005), ce résultat suggère que la coercition sexuelle est une stratégie de reproduction efficace pour les mâles, bien qu'une analyse plus détaillée soit maintenant nécessaire afin de confirmer la relation entre la coercition et le succès reproducteur des mâles. Chez d'autres primates, les mâles dominants utilisent, de la même manière, des stratégies coercitives à long terme pour limiter la polyandrie des femelles et leur imposer une proximité spatiale plus étroite (par exemple, les babouins hamadryas: Swedell and Schreier, 2009). Cependant, chez d'autres espèces, comme les orang-outans, les mâles subordonnés seraient plus coercitifs et utiliseraient plus souvent des copulations forcées que les mâles dominants (Kunz et al., 2021b). L'utilisation de stratégies coercitives peut être plus difficile pour les mâles subordonnés chez les espèces vivant en groupe par rapport aux espèces solitaires, comme les orang-outans, si d'autres membres du groupe, y compris le mâle alpha, interviennent occasionnellement pour défendre la victime.

Les femelles de haut rang reçoivent en particulier plus d'agressions que les femelles de bas rang, ce qui peut refléter les préférences d'accouplement des mâles, car les femelles dominantes présentent de meilleures performances reproductives que les subordonnées (Setchell et al., 2002; Dezeure, Charpentier, and Huchard, 2022). De même, les hyènes mâles s'accouplent préférentiellement avec des femelles de haut rang (Szykman et al.,

2001; Keddy-Hector, 1992). Ce résultat indique que la coercition est plus intense pour les femelles les plus attractives, comme chez les chimpanzés (Muller et al., 2007).

Une question importante reste de savoir si et comment les femelles mandrills peuvent naviguer dans un paysage reproductif coercitif tout en parvenant à exprimer un choix de partenaire (Setchell, 2016). Les études sur les chimpanzés ont donné des résultats contrastés, en révélant une coercition sexuelle intense dans certaines populations (Muller et al., 2007; Watts, 2022) versus des femelles capables d'exercer un choix de partenaire dans d'autres populations (Stumpf and Boesch, 2006; Kaburu and Newton-Fisher, 2015). Par conséquent, il reste possible que la coercition sexuelle puisse coexister avec une certaine capacité des femelles à exercer un choix de partenaire, comme c'est le cas chez les humains Basile, 2002; Puts, 2010. Plusieurs mécanismes peuvent permettre aux femelles d'atténuer les contraintes imposées par la coercition des mâles. Elles peuvent apaiser les agresseurs pour limiter les risques d'escalade et de blessures (Swedell and Schreier, 2009; Baniel et al., 2021), lutter contre les agresseurs ou fuir. Les mandrills femelles peuvent utiliser certaines de ces stratégies car leur répertoire comportemental consiste à éviter les approches des mâles, à se coucher lorsque les mâles tentent de s'accoupler avec eux, à refuser certaines tentatives d'accouplement (Setchell, 2016; Setchell, 2005), à interrompre la copulation en s'enfuyant (observation personnelle MJEC) voire même à former des coalitions violentes contre les mâles de haut rang (Setchell, Knapp, and Wickings, 2006; observation personnelle NS).

Liens sociaux et coercition sexuelle

Tout d'abord, nos résultats suggèrent que les femelles qui nouent des relations d'affiliation plus fortes avec certains mâles reçoivent plus de coercition de la part de ces mêmes mâles, conformément aux études chez les humains, où la coercition sexuelle s'exprime fréquemment sous forme de violence conjugale (Basile, 2002). Par ailleurs, nos résultats suggèrent que les femelles ayant des liens d'affiliation forts, soit avec les mâles du groupe, soit avec leur principal partenaire social mâle, reçoivent autant voire plus de coercition sexuelle de la part de leur mâle favori mais aussi de la part de tous les autres mâles. Ceci suggère

que les mâles peuvent agresser davantage les femelles liées à d'autres mâles, probablement dans un contexte de compétition mâle-mâle. Cependant, contrairement aux études chez d'autres primates, où les liens hétérosexuels affiliatifs protègent les femelles et leurs bébés du harcèlement par les conspécifiques (Palombit, 1999), les femelles mandrills ne semblent pas former de telles 'amitiés' avec les mâles, ou du moins celles-ci ne les protègent pas de la coercition sexuelle. L'immigration saisonnière des mâles mandrills peut expliquer, en partie, cette caractéristique, étant donné que les relations femelle-mâle ne durent généralement pas plus d'une saison de reproduction et que, par conséquent, les mâles mandrills comme femelles n'ont peut-être pas le temps de former de telles relations, ou celles-ci ne sont pas suffisamment bénéfiques. De plus, étant donné que le mâle le plus coercitif est souvent le mâle alpha, les 'amis' mâles subordonnés pourraient probablement subir des risques élevés en protégeant leurs partenaires femelles.

Bien que des études antérieures montrent que l'intégration sociale des femelles peut réduire le harcèlement par les mâles (Cameron, Setsaas, and Linklater, 2009) et que l'intégration sociale a des impacts bénéfiques sur la valeur sélective des femelles chez de nombreuses espèces (Henazi and Barrett, 1999; Silk, Alberts, and Altmann, 2003), les résultats présentés suggèrent, au contraire, que les femelles mandrills les mieux intégrées socialement reçoivent plus de coercition. Nos résultats s'ajoutent à une poignée d'études suggérant que les liens sociaux ne sont pas exclusivement bénéfiques mais peuvent être aussi associés à des coûts (réduction de la survie de la progéniture chez (Menz et al., 2020) ou longévité réduite (Blumstein et al., 2018).

Conclusion

Même si les mâles restent largement dominants sur les femelles dans la société des mandrills, ces résultats contribuent à un ensemble de nouvelles études qui dessinent un paysage plus dynamique des relations de pouvoir mâles-femelles (Surbeck and Hohmann, 2013; Young et al., 2017; Lewis, 2018; Davidian et al., 2022) dans lequel la domination intersexuelle (i) n'est pas binaire, avec des sociétés strictement dominées par les mâles versus d'autres sociétés dominées par les femelles, mais varie tout au long d'un continuum, (ii) n'est pas un attribut fixe d'une espèce mais peut fluctuer au cours du temps et selon

les contextes. Le présent travail suggère, en particulier, que les femelles peuvent parfois dominer certains mâles, même chez ces espèces présentant un dimorphisme de taille prononcé ou chez les espèces où les mâles sont sexuellement coercitifs. Des recherches supplémentaires devraient éclairer les effets potentiels - ou l'absence d'effets - d'un gain de pouvoir des femelles sur les patrons de choix du partenaire en testant si les femelles qui dominent plus de mâles sont mieux à même d'exprimer des choix reproducteurs, ou sont moins vulnérables à la coercition ou à l'infanticide.

Le présent travail rapporte également des preuves supplémentaires de l'existence d'intimidation sexuelle chez une espèce où les mâles ne sont pas manifestement agressifs à leur égard (du moins du point de vue de l'observateur humain). Le découplage temporel entre l'agressivité de mâles et la copulation explique pourquoi l'intimidation sexuelle a peut-être longtemps été négligée, alors qu'elle apparaît de plus en plus comme un phénomène comportemental important qui façonne la structure sociale et le système d'accouplement des mammifères polygynandres (Clutton-Brock, 2021). Les femelles mandrills peuvent également faire l'expérience de compromis entre les bénéfices liés à leurs relations sociales et la coercition sexuelle qu'elles subissent. Les travaux futurs devront faire la lumière sur la nature des mécanismes procurant un avantage en termes de valeur sélective pour ces femelles qui sont mieux connectées socialement, ainsi que sur l'intensité des compromis avec les coûts suscités par la coercition sexuelle. Plus généralement, les études sur les espèces sexuellement coercitives devront tenter de mesurer les coûts de la coercition sexuelle et décrire les mécanismes et stratégies qui peuvent permettre aux femelles d'exprimer des choix de partenaire.

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Appendix 1: Sex and Dominance: How to Assess and Interpret Intersexual Dominance Relationships in Mammalian Societies

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Abstract

The causes and consequences of being in a particular dominance position have been illuminated in various animal species, and new methods to assess dominance relationships and to describe the structure of dominance hierarchies have been developed in recent years. Most research has focused on same-sex relationships, however, so that intersexual dominance relationships and hierarchies including both sexes have remained much less studied. In particular, different methods continue to be employed to rank males and females along a dominance hierarchy, and sex biases in dominance are still widely regarded as simple byproducts of sexual size dimorphism. However, males and females regularly compete over similar resources when living in the same group, and sexual conflict takes a variety of forms across societies. These processes affect the fitness of both sexes, and are mitigated by intersexual hierarchies. In this study, we draw on data from free-ranging populations of nine species of mammals that vary in the degree to which members of one sex dominate members of the other sex to explore the consequences of using different criteria and procedures for describing intra- and intersexual dominance relationships in these societies. Our analyses confirmed a continuum in patterns of intersexual dominance, from strictly male-dominated species to strictly female-dominated species. All indices of the degree of female dominance were well correlated with each other. The rank order among same-sex individuals was highly correlated between the intra- and intersexual hierarchies, and such correlation was not affected by the degree of female dominance. The relative prevalence of aggression and submission was sensitive to variation in the degree of female dominance across species, with more submissive signals and fewer aggressive acts being used in societies where female dominance prevails. Thus, this study provides important insights and key methodological tools to study intersexual dominance relationships in mammals.

Introduction

When the Norwegian zoologist Thorleif Schjelderup-Ebbe (1922) published his dissertation on the social psychology of chicken a century ago, he was the first to report that

the directionality and consistency with which hen peck at each other during feeding and resting yields a stable arrangement among individuals that he called a pecking order. As in other species, dominance relationships among chicken are established and maintained through agonistic interactions whereby one individual may exhibit aggressive behavior, whereas the partner either displays submissive behavior or avoids confrontation with the aggressor altogether (Rowell, 1974). Other, structurally more complex types of hierarchies have since been described for various animal societies in which individuals recognize individual conspecifics and remember the outcome of previous agonistic interactions with co-residents (Reddon et al., 2021). Whereas solitary or unfamiliar animals can also establish a dominance relationship without prior interaction, for example, based on mutual assessment of body size, ornaments or other intrinsic cues of fighting ability, we are here primarily interested in this aspect of the social structure of species that live in permanently bisexual groups because social dominance represents a prominent feature of many animal societies.

Dominance relationships have various determinants that are not mutually exclusive and can feed back upon each other in determining the outcome of an agonistic interaction (Dehnen et al., 2022). First, in some species, a given dyadic dominance relationship reflects differential social support received by each member of the dyad (Clutton-Brock and Huchard, 2013a,b), either in the form of parental (Holekamp and Smale, 1991) or non-parental support (Schülke et al., 2010). Second, memories of previous interactions with known individuals can promote a learning effect that leads individuals to exhibit submissive behavior towards certain other conspecifics (Guhl, 1968). The effect of this dyadic interaction-outcome history is further reinforced by the winner-loser effect (Chase et al., 1994), according to which winning increases the probability to be victorious again and losing makes it more likely that the victim loses again in the next fight against any other opponent (Rutte et al., 2006; Franz et al., 2015). Finally, dominance relationships are often based upon an asymmetry in agonistic power grounded on intrinsic attributes, such as physical superiority, fighting ability, motivation or leverage that are often age-based (Hand, 1986; Lewis, 2002; Jonart et al., 2007; Dunham, 2008; Clutton-Brock and Huchard, 2013a,b; Dehnen et al., 2022; Tibbets et al., 2022). In species with pronounced sexual size dimorphism and/or elaborate weapons, these intrinsic attributes are linked to sex, with members of the larger and/or better armed sex often using their attributes to establish

and stabilize dominance relationships with members of the opposite sex (Kappeler, 1993; Lewis, 2018), just as size and strength are important determinants of within-sex dominance. However, recent evidence highlighted that sex differences in physical attributes may often fail to predict who is dominant in an intersexual relationship, as in bonobos (*Pan paniscus*) and spotted hyenas (*Crocuta crocuta*) (Surbeck and Hohmann, 2013; Vullioud et al., 2019).

In species in which groups consist of permanently associated males and females, past research has often focused on intrasexual dominance relations because they are thought to mediate access to fitness-limiting factors, such as mates and resources. As a result, most previous studies of dominance hierarchies have been framed in separate theoretical frameworks. Studies of female dominance relations focused on the ecological drivers of interspecific variation (Sterck et al., 1997; Clutton-Brock and Janson, 2012). Studies of male dominance relationships, in contrast, focused on their functional outcomes for mating access and reproductive skew (Cowlshaw and Dunbar, 1991, Alberts, 2012). Such a binary approach overlooks the potential importance of intersexual agonism for the fitness of both sexes, however. First, when males and females live in the same group, competition can occur both within and between the sexes for access to various resources, including – but not necessarily limited to – the feeding context (Valé et al., 2020; Koenig et al., 2022). Second, sexual conflict is nearly ubiquitous, and takes various forms that all generate intersexual strife (Chapman et al., 2003; Davidian et al., 2022), which affects the fitness of both sexes and may be mitigated by intersexual hierarchies. Thus, while it may make sense to use separate intrasexual hierarchies for species with pronounced sexual size dimorphism, with sex differences in the steepness, linearity and stability of the within-sex hierarchies, and in which the mechanisms of rank acquisition differ between the sexes, this approach may not be appropriate for other species.

IA few studies indicate that sex is one key variable for scrutinizing dominance hierarchies in more detail. First, in some species individuals are distributed within a group's hierarchy as a function of their sex, with either all or most males outranking all females or – more rarely – vice versa (Kappeler, 1993; Smuts and Smuts, 1993; Stevens et al., 2007; Surbeck and Hohmann, 2013; Izar et al., 2021). Such sex clusters likely reflect sex differences in morphology, physiology or life-history that underlie agonistic power and there-

fore offer an opportunity to identify sex-specific determinants of dominance. Second, males and females compete for different resources, and may therefore employ different strategies to establish and maintain their dominance rank among their same-sex peers, with unknown consequences for the establishment of intersexual hierarchies. Notably, the steepness, linearity and stability of the male and female hierarchies often differ. In chimpanzees and gorillas, for example, males have conspicuous and relatively despotic dominance hierarchies, whereas dominance relations among females are more elusive and are based on age-based queuing conventions (Stevens et al., 2007; Foerster et al., 2016). In Barbary macaques, the opposite pattern has been found, with males being more egalitarian and females more despotic in dominance style (Preuschoft et al., 1998; Hemelrijk and Gygax, 2004). Contrasting hierarchies across dyads of same- and opposite-sex members can therefore reveal informative subtleties on sex differences in social competition beyond species differences. Finally, the mechanisms of rank acquisition may differ between the sexes, with males typically relying on intrinsic attributes to compete for high rank, whereas female ranks tend to depend more often on social support (Clutton-Brock and Huchard, 2013b; Holekamp and Smale, 1991).

Nonetheless, dominance relationships between the sexes have not received the same theoretical and empirical attention as same-sex dominance relationships. Because male-biased sexual dimorphism is widespread among mammals (Lindenfors et al., 2007) and represents a default expectation based on conventional sex roles, the ability of males of these species to dominate females was typically considered an unavoidable side-effect of physical superiority and greater aggressiveness, rather than as an adaptive trait *per se* (Kappeler, 1993; Smuts and Smuts, 1993; Lewis, 2018). In contrast, the rare cases of female dominance often required special explanation and generated several hypotheses that typically invoke taxon-specific factors to explain the evolution of this sex role “reversal” (Jolly and Small, 1984; Richard and Dewar, 1991; van Schaik and Kappeler, 1996; Wright, 1999; Dunham, 2008; Kappeler and Fichtel, 2015). These few taxa or studies were not deemed of enough general interest, however, to prompt a general synthesis of intersexual relationships.

The dichotomous classification of species as either male- or female-dominated has been challenged by more recent studies indicating that these patterns only represent the end-

points of a continuum (Hemelrijk et al., 2008, 2020; Kappeler et al., 2022; Davidian et al., 2022). It is now more widely appreciated that there are taxa where members of one sex only win a proportion of all agonistic interactions with the members of the other sex or where they dominate only some, but not all, opposite-sex individuals (Surbeck and Hohmann, 2013; Young et al., 2017, Vulllioud et al., 2019; Hemelrijk et al., 2020). In addition, different methods continue to be employed to rank males and females along a dominance hierarchy (Pereira and Kappeler, 1997; Hemelrijk et al., 2008), potentially obscuring interesting biological patterns. In order to analyze this variation in a comparative fashion, comparable data on intersexual dominance relationships are required. However, existing studies have used various methods for recording details of agonistic interactions, for inferring dominance relationships, and for determining dominance hierarchies, and different species use different types and variable proportions of acts and signals to establish dominance relationships, thereby hampering comparative studies on this topic. We are therefore only beginning to explore whether different methods to analyze agonistic interactions are equivalent or whether some methods should be preferred or discouraged (Sánchez-Tójar et al., 2018; Vilette et al., 2020).

The general aim of this study is, therefore, to systematically determine the consequences of using different behavioral data, criteria and methods for inferring patterns of intersexual dominance relationships. Specifically, we aim to make recommendations about standardized methods of data collection and analyses for future studies of intersexual dominance relationships that go beyond taxon-specific idiosyncrasies. We are also interested in possible similarities across species in the nature and pattern of intersexual dominance relationships. For instance, it remains unknown whether an individual's position in the intrasexual hierarchy relates to its position in the intersexual hierarchy and, hence, whether intersexual dominance patterns are an emergent property of intrasexual ones.

To this end, we have collated datasets from nine mammalian species which were chosen because they differ in the degree to which members of one sex dominate the members of the other sex, ranging from complete male dominance to complete female dominance. Our aim was to explore the consequences of using different criteria and procedures for describing intra- and intersexual dominance relations in this sample of animal societies

and not a comparative study across a wide range of taxa and social systems. Most of these datasets are based on observations spanning at least a full year for at least two different groups, thereby accounting for seasonal variation and group idiosyncrasies. With this dataset, we (1) calculated and compared different indices of the degree of intersexual dominance in a group, (2) examined whether an individual's rank in the same-sex hierarchy predicts its position in the intersexual hierarchy, i.e., whether high-ranking females in the female hierarchy are more likely to dominate males, for example, and if the degree of correlation between intra- and intersexual hierarchy changes along the intersexual dominance spectrum, and (3) explored whether within- and between-sex conflicts differ in nature and intensity in terms of their reliance on aggressive and submissive behavior along the intersexual dominance spectrum. Taken together, our study provides a first set of recommendations and predictions for future studies aimed at explaining interspecific variation in intersexual dominance.

Methods

Study species and data collection

Data on agonistic interactions were collected from nine different mammalian species: spotted hyenas (*Crocuta crocuta*), rock hyraxes (*Procavia capensis*) and seven primates including two lemurs: Verreaux's sifakas (*Propithecus verreauxi*) and redfronted lemurs (*Eulemur rufifrons*), four Old World monkeys: chacma baboons (*Papio ursinus*), crested macaques (*Macaca nigra*), mandrills (*Mandrillus sphinx*) and vervet monkeys (*Chlorocebus pygerythrus*) and one ape: bonobos (*Pan paniscus*), as part of nine long-term individual-based field studies, including the Ngorongoro Hyena Project, Ein Gedi Rock Hyrax Research, Kirindy Forest Lemur Project, Tsaobis Baboon Project, Macaca Nigra Project, Mandrillus Project, Inkawu Vervet Project and the Kokolopori Bonobo Research Project. All studies were approved and authorized by the respective national authorities. The localization and ecology of each field site, as well as the demographic, life-history and behavioral monitoring of each study population are described in the Supplementary Materials, alongside the species-specific agonistic behavioral repertoire.

Data on agonistic interactions were recorded as detailed in the Supplementary Materials and grouped by year for each species and study group, yielding 24 group-years of data (range 1-4 per species). An agonistic interaction was defined by the expression of at least one species-specific agonistic behavior (see Hausfater, 1974). Following Deag (1977), agonistic behavioral elements were functionally characterized as either aggressive or submissive (see also Walters, 1980). Structurally, we distinguished between acts, which involve physical contact or locomotion, such as lunging or fleeing, and visual or vocal signals, such as non-physical threats or grimacing (see Pereira and Kappeler, 1997). We considered only dyadic interactions between adult individuals.

Group size ranged between 4 and 72 adult individuals, including 1 - 62 females and 2 - 26 males (Table 1). For each dataset, the corresponding co-author(s) entered the data into a standardized template. In this template, we entered only dyadic interactions and each agonistic interaction constituted a row. For each agonistic interaction, we entered the following information: 1) the identity of the two participants, 2) the sex of each participant, 3) whether the conflict was decided (i.e. only one opponent exhibited submissive behavior) or not, 4) the identity of the winner of a decided conflict, and 5) whether one or the other or both individuals displayed an aggressive act, an aggressive signal, a submissive act and/or a submissive signal (see Figure S1; Supplementary Material).

The final dataset comprised a total of 11499 agonistic interactions, including 5453 interactions between females, 2373 interactions between males, and 3673 interactions between males and females. The majority of all agonistic interactions (10,005 or 87%) were decided. The total number of interactions per group ranged from 8 to 3650 (mean \pm SD = 479.1 ± 764.9 , Table 1).

Indices of intersexual dominance

We computed hierarchies based on David's scores and I&SI, using the function 'DS' and 'ISI' of the R package 'EloRating' (Neumann et al., 2011). David's score is calculated based on power relationships between individuals, and the score of each individual is calculated based on the proportion of conflicts won and lost with other individuals in the group. For this metric, the number of conflicts is of importance because David's score

does not simply provide an ordinal rank but yields power differences between individuals. However, for the purpose of our study, we only used David's score to establish individual rank order (with the highest score receiving rank 1, the second highest rank 2, etc.). One drawback of David's score is that it is relatively sensitive to the percentage of missing dyads in the matrix and to differences in observation time between individuals (Neumann et al., 2011). I&SI, on the other hand, is based on multiple iterations of randomization of the interaction matrix, until reaching the most parsimonious rank order. The advantage of this method is that it is designed to provide ordinal rank order and is less sensitive to missing data. One drawback, however, is that it may provide several equally likely rank order solutions with large datasets and in particular when interactions are lacking for a large proportion of dyads, potentially complicating the interpretation and limiting replicability. In fact, re-running the algorithm several times on the same matrices does not provide exactly the same result.

For each hierarchy, we then calculated the percentage of males dominated by each female ("the degree of female dominance") and averaged this percentage across all females to obtain two indices.

Index 1: average percentage of males in a group dominated by each female (Hemelrijk et al., 2008, 2020) using hierarchies based on male-female interactions only. This index was calculated twice, once using David's score (de Vries, 1998) to calculate the hierarchy (Index 1a) and once using hierarchies based on I&SI (de Vries, 1998, Index 1b).

Index 2: the female dominance index, FDI (Hemelrijk et al., 2020), calculated as the average percentage of males in a group dominated by each female using hierarchies based on all agonistic interactions (i.e., inter- and intrasexual conflicts). We also computed this index twice, using hierarchies based on either David's score (Index 2a) or I&SI (Index 2b).

To evaluate whether alternative estimates of the degree of female dominance or methodological differences in calculation may alter assessment of intersexual dominance relationships, we calculated three additional indices as follows:

Index 3: percentage of intersexual conflicts won by females, calculated for each female and averaged across all females.

Index 4: percentage of intersexual conflicts won by females in each intersexual dyad averaged across all heterosexual dyads.

Index 5: total percentage of intersexual conflicts won by females overall. We then compared the correspondence among these indices by calculating pair-wise Spearman correlation coefficients for each species.

Correspondence between intra- and intersexual hierarchies

Next, we examined whether the assignment of individual rank is sensitive to the type of data used to calculate dominance hierarchies. We constructed three separate hierarchies: a female-only hierarchy based on female-female interactions only, a male-only hierarchy based on male-male interactions only, and an intersexual hierarchy based on all decided agonistic interactions. We constructed these hierarchies using David's scores since they allow for reproducibility of the analyses (i.e. the same hierarchy is obtained from the same interaction matrix each time, which is not the case with I&SI method since it is based on matrix randomization). We then extracted the ordinal dominance rank of each female (i.e., between 1 and N, N being the number of females in the group) among all other females in the intersexual hierarchy. We then calculated the Spearman rank correlation coefficient between female ordinal ranks from the intrasexual versus intersexual hierarchies. We repeated this process for males, yielding two correlation coefficients per group-year: one for female-only hierarchies and one for male-only hierarchies.

For all three (female-only, male-only and intersexual) hierarchies of each group, we compiled an index of triangular transitivity, using the function 'transitivity' in the R package 'EloRating' (Neumann et al., 2011), which provides an index of hierarchical linearity based on the proportion of triads in the hierarchy that have transitive dominance relationships (Shizuka and McDonald, 2012). Indices below 0.75 indicate that hierarchies are less transitive than random, and an index of 1 reflects a completely transitive hierarchy. We resorted to using triangular transitivity since it is less sensitive to missing data than alternative measures of linearity (h and h' ; Shizuka and McDonald, 2012; Neumann et al., 2018).

We used two separate generalized linear mixed models (GLMMs) to assess whether the degree of female dominance in a group is sensitive to differences in individual rank as a result of using either intra- or intersexual hierarchies for both, females (Model 1a) and males (Model 1b). In Model 1a, each correlation coefficient of the females' ranks between the intra and the inter-sexual hierarchy for each group-year constituted a data point; the same applies to correlation coefficients for males in Model 1b. We used separate GLMMs with beta error structure because the response in each model was bound between 0 and 1. We transformed the response using the following formula, recommended for models using a beta error distribution because it transforms zeros (which cannot be handled by beta models) into very small non-zero values (Smithson and Verkuilen, 2006):

$$x' = (x * (N - 1) + 0.5) / N$$

where x' is the transformed value of x (here the correlation coefficient) and N the sample size.

In each model we used the degree of female dominance in the group (as expressed by Index 1a) as test predictor. Note that all five indices of intersexual dominance were found to be highly correlated (see Results). We added as control predictor the percentage of male-female dyads that did not interact since this can influence David's scores (see above) and, therefore, the difference in ranks in the intra- versus intersexual dominance hierarchy. We could not include other control predictors, such as group size or adult sex ratio (cf. Hemelrijk et al., 2008; Kappeler, 2017), because of our small sample size (only 21 data points in Models 1a and 24 data points in Model 1b) to avoid overparameterization. In addition to the fixed effects we added species as a random effect to account for the non-independent repeated measures on several groups of the same species.

The form of agonistic interactions in male- versus female-dominated societies

Finally, we assessed whether the degree of female dominance in a group covaries with variation in the form of agonistic interactions within and between the sexes. More specifically, we used four GLMMs to test whether the degree of female dominance influenced

the likelihood of at least one of the two opponents exhibiting an aggressive act (Model 2a), an aggressive signal (Model 2b), a submissive act (Model 2c) or a submissive signal (Model 2d) in an agonistic interaction. For each model, we counted both decided and undecided agonistic interactions in which it was clear whether one or both individuals exhibited an agonistic act or signal ($N = 11492$ interactions). We used GLMMs with binomial error structure to model whether an act or signal was produced (Y/N) during each agonistic interaction. As test predictors, we included the degree of female dominance as quantified by index 1a, the dyad type (FF, MM, FM) and their interaction. We fitted this interaction term to test whether the effect of the degree of female dominance on the likelihood to engage in certain acts or signals differed across the three dyad types. Group size and adult sex ratio were included as control predictors in each model because they can influence social dynamics (Hemelrijk. et al., 2008; Kappeler, 2017). To account for the non-independence of repeated observations involving the same individuals, dyads and species, we added the four following random effects in each model: species, identity of the actor in the interaction, identity of the recipient and identity of the dyad. For Model 2d, the incorporation of group size as a control variable created some instability in the model preventing us from obtaining meaningful estimates for the effect of the test predictors. We therefore reran the model without group size as a variable and present the results of this second model.

While the behaviors coded as submissive acts and signals and aggressive signals were broadly similar across all the study species (see Supplementary Materials), the behaviors coded as aggressive acts differed for some datasets. In particular, displacement was considered an aggressive act in all datasets except two, the crested macaque and spotted hyena datasets. In the latter, displacement was only considered an aggressive act if the approaching individual expressed an aggressive signal. This divergence may reflect meaningful differences in the context and function of displacement behavior and variation in aggressiveness. To account for this different coding and to assess whether it had any impact on the conclusions drawn, we re-ran Model 2a (Model 2a bis) using a reduced dataset excluding crested macaque and spotted hyena datasets.

Statistical software and model assumption checking

We ran all statistical models in R 4.1.2 (R Core Team, 2021), using the function “glmmTMB” from the package glmmTMB (Brooks et al., 2017) for Models 1a and 1b, and the function “glmer” from the package lme4 (Bates and Maechler, 2010) for Models 2a-2d and 2a bis. For mixed-effects models, we included the maximum random slope structure between each fixed predictor (test and control) and each random effect (Baayen et al., 2008; Barr et al., 2013). In each model, we tested for the overall significance of the test predictors by comparing the full model to a reduced model comprising all control predictors, all the random effects and random slopes, but without any test predictor, using a likelihood ratio test (LRT, Dobson, 2002). We then assessed the significance of each predictor using a LRT between the full model and a reduced model comprising all predictors except the one to evaluate. We repeated this process across all variables using the drop1 function. For each model, we tested for collinearity issues between our predictor variables using the function vif from the package “car” (Fox and Weisberg, 2011). Collinearity was not an issue (all vifs < 3). We also assessed model stability removing one level of each random effect at a time and recalculating the estimates of the different predictors that revealed no stability issue (except for model 2d, see above). Finally, we tested for overdispersion in Models 1a and 1b, which was not an issue (all dispersion parameters < 1.08). For Models 2a-d and Model 2a bis, we calculated the marginal R^2 (i.e., the variance explained by the fixed effects) and the conditional R^2 (i.e., the variance explained by the entire model including both fixed and random effects) using the function *r.squaredGLMM* of the package “MuMin” (Barton, 2020). For Models 1a and 1b we could not compile the R^2 due to negative model’s distribution-specific variance.

Results

The interaction matrices compiled for this study were highly heterogeneous in terms of missing dyads, from being almost full, with most dyads interacting with each other, as in the Ekalakala bonobo group, to being largely empty, with interactions absent for >85% of dyads, as in the mandrill or rock hyrax groups (Table 2; Tables S1-S3). Most inter- and

intrasexual hierarchies were highly transitive (transitivity index ≥ 0.97 , Tables 2 and S1-S3), but a few hierarchies had a transitivity index close to the random level of transitivity set at 0.75 as in redfronted lemurs (group X) or well below this random level as in rock hyraxes (group Isiim) (Table 2). There were no strong correlations between the degree of female dominance and the degree of transitivity (correlation coefficient = 0.07, Figure S2).

Indices of intersexual dominance

The species included in this comparative study represent a continuum in terms of the degree of intersexual dominance, from strictly male-dominated species as in the two chacma baboon groups (all indices ≤ 0.09 % group males dominated by each female), to strictly female-dominated species as in the three Verreaux's sifaka groups (all indices ≥ 0.94 , Figures 1 and 2, Table S4). Importantly, our dataset does not comprise only species at the extreme ends of the spectrum of intersexual dominance but also several species where dominance is not very biased towards one sex (e.g. some redfronted lemur, bonobo or vervet monkey groups, Figures 1 and 2, Table S4).

All five female dominance indices correlated strongly with each other (Spearman R2 range: 0.92-0.98, Figures 1 and 2), indicating that different indices of female dominance can be used interchangeably, as they do not influence the position of each group/species on the spectrum of the extent of female dominance. Please note however that for datasets with a large proportion of missing dyads the different indices provided more variable values (Figure 2 and Tables S1-S3).

Correspondence between intra- and intersexual hierarchies

In models 1a and 1b, the full model was not significantly different from the null model (Model 1a: N= 21 group_years, df = 1, $\chi^2 = 0.096$, P = 0.756; Model 1b: N= 24 group_years, df = 1, $\chi^2 = 1.613$, P = 0.204) indicating that variable degrees of intersexual dominance did not significantly impact the differences in dominance rank observed between the intra- and the intersexual dominance hierarchy for both males and females (Table S5,

Figure 3). These changes were rather influenced by the structure of the datasets, at least for the female hierarchies in which correlation between the intra- and the intersexual dominance hierarchies were influenced by the percentage of missing dyads ($P=0.051$, Table S5). Nevertheless, overall, intra- and intersexual hierarchies were highly correlated, across variable degrees of intersexual dominance, especially for females (Figure 3).

Differences in agonistic interactions in female vs male-dominated societies

Individuals in most study species used acts more than signals in agonistic interactions, with some species, like redfronted lemurs and bonobos, using acts almost exclusively (Table 2). Verreaux's sifakas diverge from this general trend: they used acts and signals equally in one group and signals more often than acts in the two other groups. Together with mandrills, Verreaux's sifakas are also the study species using the highest ratio of submissive to aggressive behaviors.

The full model was significantly different from the null model in three out of four models testing the effect of the degree of female dominance and of the dyad type (M-F, F-F, M-M) on the probability of using aggressive and submissive acts or signals ($N_{interactions} = 11.492$, $N_{dyads} = 2908$, $N_{individuals} = 508$, LRT, $df=5$, Model 2a: $\chi^2=34.97$, $P < 0.001$; Model 2b: $\chi^2=57.25$, $P < 0.001$; Model 2c: $\chi^2=8.30$, $P = 0.141$, and Model 2d: $\chi^2=37.15$, $P < 0.001$). In Model 2a investigating the probability of using aggressive acts, the interaction between the degree of female dominance and dyad type was marginally non-significant ($P=0.070$, Table 4). For FM and FF dyads, the probability to use aggressive acts decreased slightly with increasing female dominance, and such decrease was steeper for MM dyads (Figure 4A and S4). We found similar results in Model 2a bis with a reduced dataset excluding crested macaques and spotted hyenas (Figure S5) with the exception that the interaction between the degree of female dominance and dyad type was significant ($P=0.001$, Table S6) and that the probability to use aggressive acts did not decrease with increasing female dominance for FF dyads. In Model 2b, we found a significant interaction between the degree of female dominance and the probability of expressing aggressive signals ($P=0.033$, Table 3). For FM and FF dyads, the probability for aggressive signals to occur in agonistic

interactions decreased with increasing degree of female dominance but remained stable for MM dyads (Figure 4B and S4). In Model 2c, the degree of female dominance and dyad type did not significantly affect the probability for submissive acts to occur during agonistic interactions (Figure 4c and S4). Finally, Model 2d revealed a significant interaction between the degree of female dominance and dyad type on the probability for submissive signals to occur ($P=0.004$, Table 3). While the probability for submissive signals to occur during agonistic interactions increased steadily with the degree of female dominance, this positive relationship was less pronounced for FM dyads compared to MM and FF dyads (Figure 4D and S4). The marginal R^2 were 0.142, 0.202, 0.050, 0.057, and 0.190 for Models 1a, 1a bis, 1b, 1c and 1d respectively. The conditional R^2 were 0.819, 0.608, 0.864, 0.531, and 0.907 for Models 1a, 1a bis, 1b, 1c and 1d respectively.

Discussion

Our study confirmed that intersexual dominance varies along a continuum from strict female dominance to strict male dominance independent of the measure used. All indices of the degree of female dominance were well correlated with each other, and the rank order among same-sex individuals was highly correlated between the intrasexual and intersexual hierarchies, and such correlation was not significantly affected by the degree of female dominance in the group. In most study groups, within sex ranks were highly correlated between the intra- and the intersexual hierarchies and variations in this correlation were function of the dataset property (i.e. % of missing dyads in Model 1a). Interestingly, the relative prevalence of each type of agonistic behavior was sensitive to variation in the degree of female dominance, with more submissive signals and fewer aggressive acts being used by both sexes and across all dyad types in societies where female dominance prevails. Below, we discuss each of these main results in light of the current knowledge of heterosexual relationships across mammalian societies.

Indices of intersexual dominance

One of the novelties of the present study was the standardized application of several methods to calculate intersexual dominance across a range of mammalian species with different social systems. We found the degree of female dominance to vary continuously from strict male dominance to strict female dominance, adding to a growing number of studies (Hemelrijk et al., 2008, 2020; Rina Evasoa et al., 2019; Kappeler et al., 2022; Davidian et al., 2022) breaking with traditional binary categorizations into female-dominant vs. male-dominant species. Clearly, binary categories are insufficient to capture the variation in intersexual dominance relationships occurring both across and within species. The latter insight is illustrated by species for which we had data from more than one group, such as bonobos, redfronted lemurs and vervet monkeys, confirming results of several recent studies (Surbeck and Hohmann, 2013; Vullioud et al., 2019; Hemelrijk et al., 2020; Izar et al., 2021). These patterns open the way for future investigations of the sources of inter- and intraspecific variation in intersexual dominance patterns.

Our study will facilitate future comparative studies by demonstrating strong positive correlations among the five indices that measure the degree of female dominance. Some indices, namely 1 and 2, required the construction of intersexual hierarchies while others, namely 3-5, simply quantified the proportion of dyadic interactions won by one sex. Their high correlation suggests that they capture the same behavioral phenomenon, and validate the use of dominance hierarchies to measure asymmetries between the sexes in the propensity to win intersexual agonistic interactions. Special care should be taken for datasets with high uncertainty induced by missing interactions for a large number of dyads, as in redfronted lemurs and rock hyraxes (Figure S3) for which female dominance indices varied greatly. However, even with such a variation, the study groups were positioned in the same area of the spectrum characterizing the degree of female dominance, regardless of the index chosen (Figure 2). Overall these indices are thus robust and consistent. This is further confirmed by the similar values generated by David's score or I&SI methods. These results indicate that all five indices capture meaningful aspects of dominance relationships between males and females, ensuring the comparability of past, present and future studies using one or several of these indices.

By positioning each study group along the intersexual dominance gradient using a standardized approach, we generated a fine-grained picture of their relative order. Such positions were largely consistent with previous descriptions of intersexual dominance for most of these species; some were already described as predominantly male dominant, like mandrills (Setchell et al., 2001), chacma baboons (Kalbitzer et al., 2015) and crested macaques (Tyrrell et al., 2020; Duboscq et al., 2013), or predominantly female dominant, like Verreaux's sifaka (Richard and Heimbuch, 1975), spotted hyenas (Vullioud et al., 2019), bonobos (Parish, 1996; Parish et al., 2000) or rock hyraxes (Koren et al., 2006, Koren and Geffen, 2009). Similarly, redfronted lemurs exhibited no sex-biased or slightly male-biased intersexual dominance as previously studied in captive and wild populations (Pereira et al., 1990; Ostner and Kappeler, 1999). The relatively balanced and flexible intersexual dominance characterizing vervet monkeys (Young et al., 2017; Hemelrijk et al., 2020) was also reported by recent studies of capuchin monkeys (Izar et al., 2021). For other groups or species, indices of female dominance contrasted with previous empirical evidence. For example, this study revealed that female dominance in bonobos is far from strict, since one group appears predominantly male dominant (Table 3). Generally, intersexual dominance relationships have been particularly well studied in the set of species selected for this study, but much remains to be learned about the generality of the patterns reported here from future studies of many other species and populations where social hierarchies have so far been examined separately for males and females.

Correspondence between same-sex and opposite-sex hierarchies

One cannot simply assume that an individual's position in the intrasexual hierarchy is directly predictive of its position in the intersexual hierarchy given the functional and structural differences between male and female intrasexual hierarchies (Clutton-Brock and Huchard, 2013b). Males and females often – but not always (Vullioud et al., 2019) – show distinct mechanisms of rank acquisition (de Waal, 1984; Holekamp and Smale, 1991; Foerster et al., 2016), as well as different hierarchical properties, such as steepness (Stevens et al., 2007) or stability (Holekamp and Smale, 1991). We found that in most cases, individuals maintained their same-sex dominance ordering in the intersexual hi-

erarchy. For example, if four males are ranked A-B-C-D in the intrasexual hierarchy, it is very likely that the rank order of these males will be maintained in the intersexual dominance hierarchy, even if some females are ranked in between or above those males. This result clarifies an important aspect of the structure of intersexual hierarchies. Like intrasexual hierarchies in most species included in this study, intersexual hierarchies are mostly highly transitive (with the exception of one group of rock hyrax and one group of redfronted lemurs, Figure S2). Intersexual ranks are simply obtained by merging both intrasexual hierarchies, respecting their initial order, but at variable levels, i.e., from a full entanglement, sometimes referred to as ‘codominance’ (Lewis, 2018), to strict male or female dominance, where all members of one sex outrank all members of the other sex. The fact that the degree of female dominance was not found to influence these patterns suggests that this effect persists across the whole gradient of intersexual dominance. Overall, individuals of both sexes can thus be ordered together in a common, meaningful intersexual hierarchy, according to their competitive abilities, whatever they might be based on. While models suggest that an individual’s experiences with the self-reinforcing effects of winning and losing fights may concern interactions with both males and females (Hemelrijk et al., 2008), this is not necessarily so, as indicated by evidence of a sex difference in the winner-loser effect in hamsters (Solomon et al., 2007).

A few social groups in our dataset showed a relatively low correlation between an individual’s position in the same-sex vs. intersexual hierarchy, as in males of one chacma baboon group, or in females of one bonobo, one crested macaque and one rock hyrax group (Figure 3). It is possible that the number of dyads for which no interaction was recorded may affect the robustness of hierarchies. Yet, this is unlikely to explain our results given that the percentage of missing dyads was included as a control factor in our models and did not yield a significant effect on the correlation between the two hierarchies. In addition, there are species and sex differences in the dynamics of hierarchies that are not accounted for here, and which may influence hierarchical properties, especially transitivity. Specifically, the methods used here to build hierarchies ignore temporal changes in hierarchies, whereas other methods continuously adjust and update a hierarchy over time when it is characterized by high temporal dynamics (e.g., use of the dynamic Elo-ranking methods: Neumann et al., 2011). Static approaches may be suitable in some cases, such as the stable, linear and heritable hierarchies of female cer-

copithecines, but less so for unstable male hierarchies in seasonal breeding species where most males are not permanent group members, as in mandrills (Brockmeyer et al., 2015) and rock hyraxes (Barocas et al., 2001), or species where males move frequently between groups, as in crested macaques (Marty et al., 2016; Neumann et al., 2011). The moderate correspondence between intra- and intersexual hierarchies may thus reflect the social dynamics in these species, which may occur over the course of a year (i.e., the time frame used here to derive hierarchies).

Different dominance styles in male- and female-dominated societies

We finally investigated whether the relative importance of agonistic acts vs. signals and of aggressive vs. submissive behavior varies across the spectrum of interspecific variation in intersexual dominance. This analysis highlighted at least two important results. First, the relative frequencies with which different agonistic behaviors were used followed the same pattern in relation to the degree of female dominance for male-male, female-female and male-female dyads. Second, and most noticeably, an increase in the degree of female dominance was related to a steep increase in submissive signals during contests and a modest decrease in the use of aggressive acts. This pattern suggests that in societies where dominance is biased towards females, signals are particularly important for structuring social life and likely limit the use of direct aggression during conflicts, compared to societies dominated by males. Nonetheless, the intensity and frequency of agonistic acts or signals can vary even between species that are positioned alongside on intersexual dominance spectrum. For example, across macaque societies, which are all largely male-dominated, there are well-described differences between species in the ratio of contact aggression and non-contact aggression, which are typically related to a species' 'dominance style', which characterizes dominance relationships from most egalitarian to most despotic (Thierry, 2007).

The relationship between the degree of female dominance and the differential use of aggression and submission might partly reflect a reduction in male aggressiveness across the female dominance gradient, along with a decreasing magnitude of sexual dimorphism. Indeed, in several species where females dominate males, their body size or levels

of aggressiveness and androgens resemble those of males – as in many lemurs (Jolly, 1984; Petty and Drea, 2015; Grebe et al., 2019), spotted hyenas (McCormick et al., 2021), rock hyraxes (Koren et al., 2006), and meerkats (Davies et al., 2016), and ongoing research confirms that the degree of sexual dimorphism is a strong predictor of the outcome of intersexual agonistic interactions across primates (Huchard et al., unpubl. data). In addition, species-specific patterns of agonistic interactions (Fig. S2) suggest that the general, interspecific relationship is largely driven by spotted hyenas and sifakas, which stand out by using fewer aggressive acts than other female-dominant species. In contrast, the increased use of submissive signals in female-dominant species is robust and involves most populations where dominance is largely female-biased, except for bonobos. Overall, female-biased dominance appears associated with a higher ratio of submissive signals to aggressive acts, a result that needs verification with a larger number of species, as well as using analyses that control for phylogenetic proximity between species. Controlling for phylogeny was here complicated by the low number of species involved, coupled with a heterogeneous phylogenetic coverage comprising a disproportionate number of primates as well as a couple of other, distantly related species.

The generality of this phenomenon across all dyad types may be compatible with the idea that agonistic interactions are ruled by convention-based norms that are shared by group members across age-sex-classes. These norms might possibly be socially transmitted, or flexibly influenced by prior experience, such as winner-loser effects (Tibbetts et al., 2022). Regardless of the underlying mechanism, these results suggest that female-dominated societies may rely less on aggression than male-dominated ones. This constitutes an important finding to identify the consequences of intersexual power for individual health, welfare and fitness, as well as for social dynamics and population demography. Our findings may also have ramifications for a better understanding of variation in the level of intra- and intersexual violence across past and contemporary human societies (Gómez et al., 2016; Glowacki et al., 2020). Other patterns are more discrete. The use of aggressive signals also covaried with the degree of female dominance in female-female and intersexual dyads, with fewer threats observed in societies where ritualized submissive signals limit the use of direct aggression; threats may therefore lose their intimidating function when they are not reinforced by direct aggression. Alternatively, it is possible that either aggressive or submissive signals are needed to maintain a dominance hierarchy

(Tibbetts et al., 2022), but that both are functionally redundant and rarely co-exist. Male-male dyads, in contrast, hardly use any threats across the continuum, possibly because it is risky to threaten a rival in male-dominant societies where male-male competition is often intense and contest-based, while threats are uncommon in female-dominant societies for the reasons discussed above. Finally, the slight (non-significant) decline of submissive acts along the female dominance gradient likely reflects the decline of aggressive acts, probably because submissive acts represent responses to aggressive acts. In contrast, aggressive acts are not systematically followed by a submissive act, which may explain why the decline is less pronounced for submissive than aggressive acts.

Conclusions and Recommendations

This study provides important insights and key methodological tools to study intersexual dominance relationships in mammals, and perhaps in other vertebrates. First, we show that several distinct quantitative indices of intersexual dominance are equally successful at ordering groups from several populations and species along an intersexual gradient ranging from strict male to strict female dominance. Second, we show that intersexual hierarchies are meaningful emergent properties of interactions occurring within and between the sexes. These hierarchies arise from merging male and female hierarchies, where individuals retain their intrasexual rank, but can be outranked by a variable number of opposite-sex group members. Third, we found continuous variation in patterns of agonistic interactions across species, characterized by less direct aggression and more ritualized submissions in female-dominant societies, which have apparently developed potent mechanisms of conflict mitigation that promote peaceful interactions and inhibit aggression. This work provides important foundations for future studies of intersexual dominance across mammals to uncover determinants and consequences of variation in intersexual dominance comprehensively, using standardized, quantitative measures within and across societies.

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Research procedures of the Tsaobis project were evaluated and approved by the Ethics Committee of the Zoological Society of London and the Ministry of Environment and Tourism, Namibia (MET Research/Collecting Permits 1786/2013 and 1892/2014), and adhered to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research and Teaching.

The *Mandrillus* project followed all applicable international, national, and/or institutional guidelines for the care and use of animals. This study further complied with ethical protocols approved by the CENAREST institute (authorization number: AR0060/18/MESRS/CENAREST/CG/CST/CSAR) and adhered to the legal requirements of Gabon for the ethical treatment of non-human primates.

The research on crested macaques adheres to all legal requirements and guidelines of the German, British, and Indonesian governments and institutions (permit numbers 1240/FR-P/SM/VI/2008 and SI-101/Set-3/2008) and to the ASAB/ABS (2012) guidelines for the Treatment of Animals in Behavioural Research and Teaching.

All study procedures of the Inkawu Vervet Project were approved by the relevant local authority “Ezemvelo KZN Wildlife” in South Africa.

Study procedures at Kirindy Forest adhered to the Guidelines for the Treatment of Animals in Behavioral Research and Teaching (Animal Behaviour 2020) and the legal requirements of the country (Madagascar) in which the work was carried out. The protocol for this research was approved by the Malagasy Ministry of the Environment.

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Data accessibility: The datasets used in this study are available in Figshare, under the link below: https://figshare.com/articles/dataset/Dataset_for_Sex_and_Dominance_How_to_Assess_and_Interpret_Intersexual_Dominance_Relationships_in_Mammalian_Societies_/19583215.

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Appendix

Figure 1: Correlations among the five female dominance indices. All pairwise comparisons among the five indices are shown, with each point representing one social group of the nine species. The 7 indices are abbreviated on the axis as follow: P. male dominated._FM_DS: percentage of males dominated by each female in the hierarchy compiled using David's score and based on heterosexual conflicts only (Index 1a); P. male dominated._FM_ISI: percentage of males dominated by each female in the hierarchy compiled using I&SI and based on heterosexual conflicts only (Index 1b); FDI_DS: female dominance index based on hierarchies compiled using David's score and based on all conflicts (Index 2a); FDI_ISI: female dominance index based on hierarchies compiled using I&SI and based on all conflicts (Index 2b); Individ. fem. dom.: Individual female dominance, percentage of intersexual conflicts won by females calculated for each female and averaged across all females (Index 3); Dyadic fem. dom.: Dyadic female dominance, percentage of intersexual conflicts won by females in each male-female dyad and averaged across all heterosexual dyads (Index 4); Overall fem. dom.: Individual female dominance, percentage of intersexual conflicts won by females over males overall across all heterosexual conflicts (Index 5). "Cor": correlation coefficient calculated using Spearman rank correlation tests.

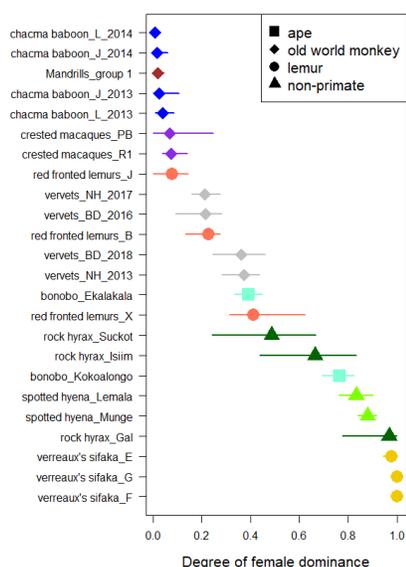


Figure 2: Distribution of the female dominance indices in the 24 study groups. Each line represents a study group during a given year. The symbol depicts the mean across all seven female dominance indices and the line the range of these indices. Each species is depicted with a different color. Apes, old world monkeys, lemurs and non-primates are depicted using squares, diamonds, circles and triangles respectively.

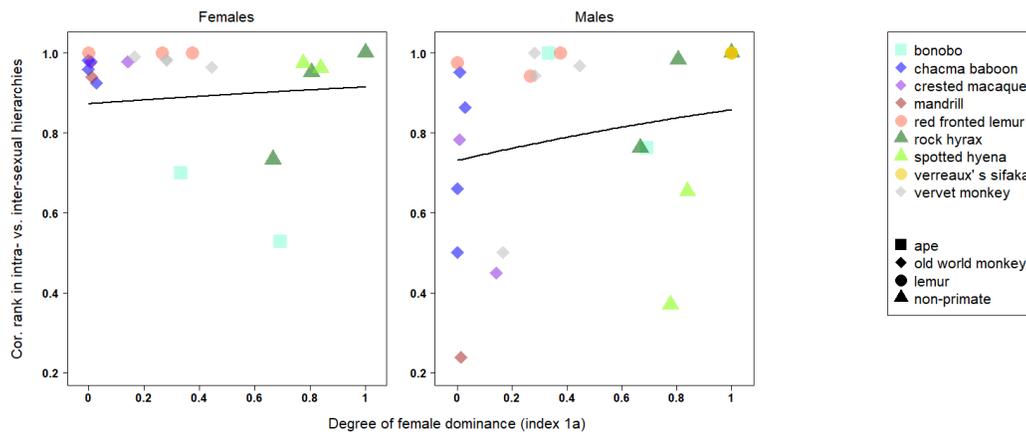


Figure 3: Degree of female dominance and correlation between intra- and intersexual hierarchies for females (left panel) and males (right panel). Each species is depicted using a different color. Apes, old world monkeys, lemurs and non-primates are depicted using squares, diamonds, circles and triangles respectively. Each dot represents one study group in a given year. The black lines indicate the model's predictive lines for the effect of the degree of female dominance on the correlation between individual ranks from the intra- and from the intersexual hierarchies for females (Model 1a, left panel) and for males (Model 1b, left panel). The lines are only indicative since the p-values for these effects were non-significant in both models. Verreaux's sifakas do not appear in the left panel since there was only one female in each of the three groups and correlations between female ranks in the intra and intersexual hierarchies could thus not be calculated.

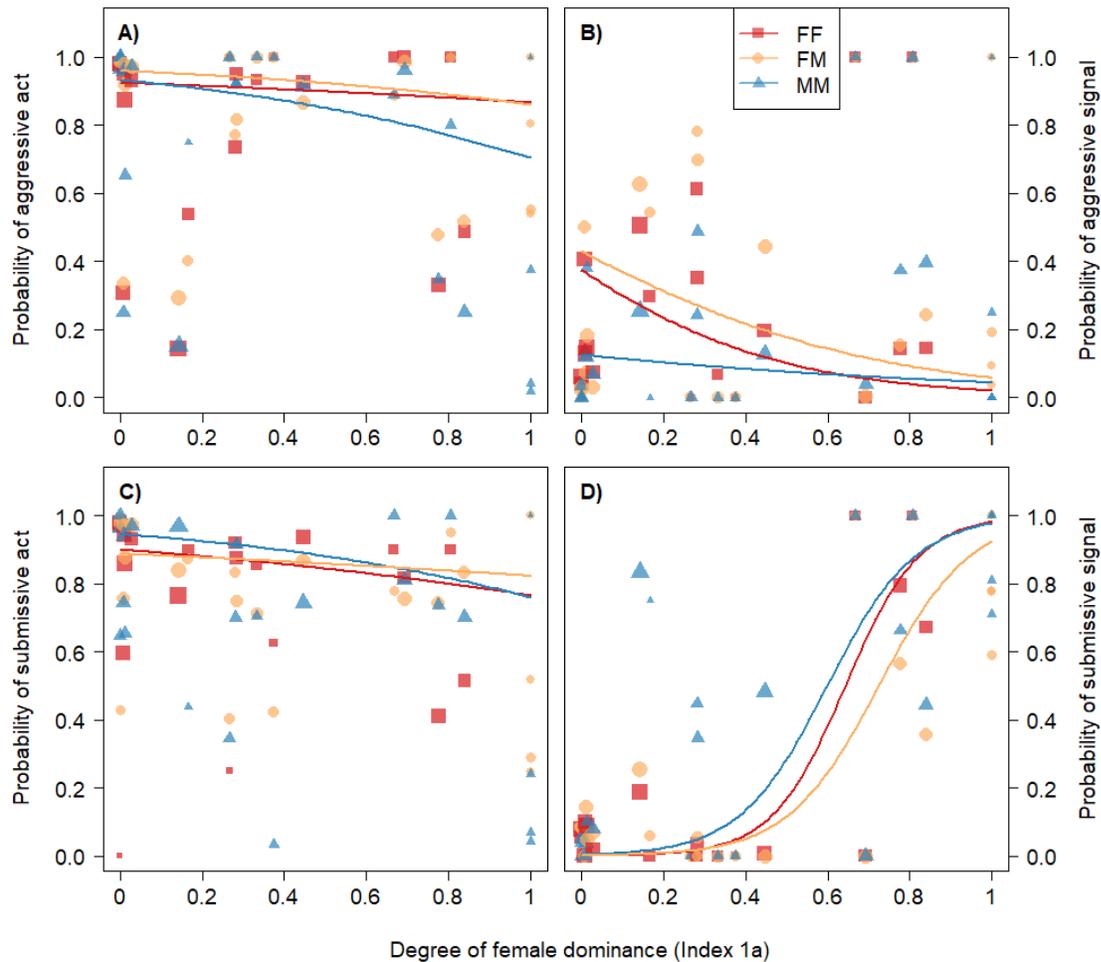


Figure 4: Influence of the degree of female dominance (Index 1a) and dyad type (FM, FF, MM) on the likelihood for conflicts to comprise aggressive acts (A), aggressive signals (B), submissive acts (C) or submissive signals (D). Each dyad type is depicted using a different color and symbol: Red square: female-female dyads (FF), orange circle: female-male dyads (FM) and blue triangle: male-male dyads (MM). Each dot represents one dyad type of a study group on a given year and dot size is proportional to the log number of dyads. Log scale was chosen here because the number of dyads in each dyad type in the largest groups were orders of magnitude larger than in smallest groups. The red, orange and blue lines depict the predicted relationship between the degree of female dominance and the likelihood of each act or signal to occur for FF, FM and MM dyads respectively. These lines are derived from Models 2a (panel A), 2b (panel B), 2c (panel C), and 2d (panel D). Please note that for Model 2c the full model did not significantly differ from the null model and the corresponding lines do not represent meaningful statistical relationships but are used for illustration.

Table 1: Summary of the data collated for this study.

Species	Group	Group size	N. females	N. males	Total N. interactions	N. interactions FF	N. interactions FM	N. interactions MM
Bonobo	Ekalakala	8	5	3	387	29	120	238
	Kokoalongo	21	13	8	580	53	254	273
Chacma baboon	J_2013	27	17	10	429	255	120	54
	J_2014	27	18	9	1076	490	489	97
	L_2013	30	19	11	368	131	171	66
	L_2014	30	20	10	1467	636	674	157
Crested macaque	PB	27	18	9	459	319	79	61
	R1	51	25	26	3650	2129	837	684
Mandrill	Group 1	72	62	10	555	331	193	31
Redfronted lemur	B	12	3	9	87	5	48	34
	J	10	2	8	46	1	16	29
	X	8	4	4	82	7	60	15
Rock hyrax	Gal	6	3	3	8	0	7	1
	Isiim	21	10	11	37	14	9	14
	Suckot	18	10	8	39	15	10	14
Spotted hyena	Lemala	26	14	12	574	390	154	30
	Munge	29	13	16	195	75	63	57
Verreaux's sifaka	E	4	1	3	48	NA	20	28
	F	4	1	3	63	NA	50	13
	G	5	1	4	59	NA	50	9
Vervet	BD_2016	17	11	6	203	79	66	58
	BD_2018	29	16	13	703	262	117	324
	NH_2013	16	11	5	238	131	30	77
	NH_2017	11	9	2	146	101	36	9

Appendix

Table 2: Characteristics of the intersexual hierarchies and conflict types used in this study.

Species	Group	N dyads	Prop. Missing dyads	Transitivity (Pt)	Ratio of act vs. signal	Ratio of submissive vs. aggressive behaviors	Prop. of decided conflicts
Bonobo	Ekalakala	28	0.04	1.00	387.00	0.78	0.62
	Kokoalongo	210	0.39	0.97	64.11	0.77	0.56
Chacma baboon	J_2013	351	0.48	1.00	10.07	0.98	0.98
	J_2014	351	0.26	0.98	7.81	0.98	0.98
	L_2013	435	0.60	1.00	9.94	0.97	0.97
	L_2014	435	0.23	1.00	5.31	0.96	0.97
Crested macaque	PB	351	0.50	1.00	2.27	1.23	0.82
	R1	1275	0.45	0.98	1.43	1.84	0.85
Mandrill	group 1	2556	0.86	1.00	3.78	0.98	1.00
Redfronted lemur	B	66	0.62	1.00	NA	0.36	0.36
	J	45	0.58	1.00	NA	0.52	0.52
	X	28	0.46	0.83	NA	0.30	0.30
Rock hyrax	Gal	15	0.67	NA	1.00	1.00	1.00
	Isiim	210	0.87	0.50	1.00	1.00	1.00
	Suckot	153	0.84	1.00	1.00	1.00	0.92
Spotted hyena	Lemala	325	0.56	1.00	1.02	1.49	0.91
	Munge	406	0.73	1.00	1.17	1.57	0.87
Verreaux's sifaka	E	6	0.17	1.00	0.32	3.54	0.96
	F	6	0.17	1.00	1.00	1.13	0.87
	G	10	0.40	1.00	0.74	1.47	0.85
Vervet	BD_2016	136	0.40	0.97	1.77	0.87	0.57
	BD_2018	406	0.43	0.99	2.23	0.95	0.71
	NH_2013	120	0.44	1.00	1.42	0.93	0.63
	NH_2017	55	0.16	0.97	2.46	1.34	0.88

NA: Transitivity could not be computed for the rock hyrax group Gal. For all redfronted lemurs, the ratio of act vs signal could not be computed since no signal has been recorded in the dataset for this species.

Table 3: Effect of the degree of female dominance and dyad type (FM, FF, MM) on the probability of using aggressive acts (Model 2a), aggressive signals (Model 2b) and submissive signals (Model 2d). Results from Model 2c explaining the probability of using submissive acts are not shown here as this model did not differ from the null model. Since all the continuous variables were standardized to a mean of 0 and a standard deviation of 1, the intercepts and corresponding main effects are indicated for an average degree of female dominance, sex ratio and group size. For all the estimates of the ‘Dyad type’ fixed effect, female-female dyads are the reference category. SE indicates the standard error of the estimate for each predictor. § indicates control predictors. Significant p-values ($p < 0.05$) are indicated in bold and trends ($p < 0.1$) in italics. CI_{low} and CI_{high} indicate the lower and upper limits of the 95% confidence intervals for the estimates of each predictor. The sample size for each model is $N_{\text{interactions}} = 11492$, $N_{\text{dyads}} = 2908$, $N_{\text{individuals}} = 508$.

Model	Response	Predictor	Estimate	SE	CI _{low}	CI _{high}	χ^2	P
2a	Did the conflict comprise an aggressive act (Y/N)	Intercept	2.37	1.25	-0.17	5.03		
		Dyad type (FM)	0.51	0.11	0.18	0.83		
		Dyad type (MM)	-0.12	0.17	-0.56	0.29		
		Degree of female dominance	-0.17	0.49	-0.97	0.82		
		Sex ratio [§]	-1.24	0.19	-1.87	-0.69	38.41	<0.001
		Group size [§]	-0.88	0.23	-1.58	-0.26	15.70	<0.001
		Female dominance * dyad type (FM)	-0.18	0.10	-0.53	0.15	5.31	0.070
		Female dominance * dyad type (MM)	-0.29	0.13	-0.71	0.12		
2b	Did the conflict comprise an aggressive signal (Y/N)	Intercept	-1.22	1.51	-4.74	1.76		
		Dyad type (FM)	0.41	0.13	0.01	0.77		
		Dyad type (MM)	-0.95	0.23	-1.54	-0.37		
		Degree of female dominance	-0.87	0.51	-1.88	-0.06		
		Sex ratio [§]	-0.05	0.22	-0.72	0.67	0.04	0.848
		Group size [§]	0.49	0.27	-0.24	1.20	3.23	0.072
		Female dominance * dyad type (FM)	0.22	0.13	-0.13	0.60	6.85	0.033
		Female dominance * dyad type (MM)	0.57	0.19	0.08	1.05		
2d	Did the conflict comprise a submissive signal (Y/N)	Intercept	-4.81	1.83	-9.34	-1.11		
		Dyad type (FM)	0.19	0.45	-1.02	1.27		
		Dyad type (MM)	1.20	0.88	-1.06	3.09		
		Degree of female dominance	2.90	0.79	1.87	4.23		
		Sex ratio [§]	0.46	0.41	-0.32	1.34	1.18	0.278
		Female dominance * dyad type (FM)	-0.56	0.27	-1.34	0.18	11.08	0.004

Supplementary Material

1. Supplementary Data

All references cited here figure in the reference list of the main text.

Study species and data collection

This section summarizes key details of the populations of bonobos, chacma baboons, mandrills, crested macaques, vervet monkeys, redfronted lemurs, Verreaux's sifakas, rock hyraxes and spotted hyenas, and how the different types of data entering our analyses were collected.

1.1 Bonobos (*Pan paniscus*) at the Kokolopori Bonobo Reserve, DRC

General information

Average body mass is 33kg for adult females and 38kg for adult males (Yapuncich et al. 2020). Maximum lifespan is estimated around 50 years, and individuals become sexually mature around 8-9 years. Average gestation length is 230 days and average interbirth interval is 4.8 years (Gruber & Clay 2016). Bonobos are frugivorous, as their diet mainly comprises fruits. They also eat substantial amounts of stems and leaves and occasionally flowers, seeds, mushroom, honey, insects, eggs, and small vertebrates (e.g., flying squirrels, duikers, monkeys).

Social system

Social organization: Bonobos live in multimale-multifemale societies with high fission-fusion dynamic. Males are mostly philopatric and females mostly disperse. Throughout the day, individuals range in mixed-sex parties of varying sizes and compositions. Bonobos use long-distance vocalizations (high-hoots) and call combinations (low hoot-high hoot) to coordinate party movements and maintain group cohesion. Bonobo groups comprise around 8 to 27 mature individuals (estimated age of 10 or above) and the pub-

lished adult sex ratio (male to female) varies across populations, ranging from 0.31 to 0.83 (Jaeggi et al. 2016).

Social structure: Female bonobos form strong and differentiated social relationships. The nature and strength of female-female relationships may differ based on the context and behavioral measures (Tokuyama & Furuichi 2016). Females often provide agonistic support to each other and potentially use female coalitions as a counterstrategy against male harassment (Tokuyama & Furuichi 2016). Males also form differentiated social relationships with other males and females within the group, but the strongest social relationships of males tend to be with their mothers. While the highest dominance ranks within groups are often occupied by females, which also seem to have feeding priority over males, there is no sex segregation in an intersexual dominance hierarchy (Surbeck & Hohmann 2013). Between-group interactions can range from brief and aggressive, to prolonged and tolerant and neighboring groups have large home range overlaps (Lucchesi et al. 2020).

Mating system: Bonobos have a promiscuous mating system. Females exhibit prolonged maximally tumescent sexual swellings and multiple females can be in oestrous simultaneously in a group. Sexual swellings are a poor indicator of ovulation and fecundity among female bonobos (Douglas et al. 2016). There is a high reproductive skew among males, with the alpha male siring most of the infants within the group (Surbeck et al. 2017). Mothers exert strong influence on mating opportunities and the reproductive success of their sons (Surbeck et al. 2019).

Care system: Infant bonobos are carried by their mothers until they are weaned at around 4-5 years old, but maternal support for males can extend till adulthood (Surbeck et al. 2019). There is currently no description of paternal care or paternal kin recognition in wild bonobos.

Observations

We conducted all-day party follows of two groups of bonobos, Ekalakala and Kokoalongo, at the Kokolopori Bonobo Reserve (RDC) from October 2016 to August 2018. There were 3 adult males and 5 adult females in Ekalakala, and 8 adult males and 13 adult females in Kokoalongo. These numbers remained the same for both groups throughout the study

period. We collected all-occurrence data on agonistic interactions that occurred in the followed party. We recorded the identity of the actor(s) and recipient(s) of agonistic interactions whenever we could, as well as the type of agonistic behavior (see below for more details).

Definitions of aggressive and submissive acts and signals

We considered aggressive acts as when an individual directed contact and non-contact aggression towards another individual (see below). We considered aggressive signals as 'threaten' and 'stand bipedal'. We determined submissive acts as when an individual fled, jumped aside, or walked away upon receiving the aggression, or when an individual avoided/gave way to another individual.

Aggressive acts

Directed drag branch: "A branch broken from a tree, or one lying on the ground is dragged by one hand during a charging display..." (Goodall 1968). Here, we only include drag branches that are clearly directed at another individual (i.e., branch is dragged right towards another individual).

Displace: Supplant or vacate another individual from his/her original location by approaching or running towards him/her. Most frequently seen during feeding.

Pester: Repeatedly approaching an individual, or group of individuals, usually accompanied by piloerection and screaming (also known as contest hoots). Usually happen upon arrival of feeding trees. Most frequently seen in young males.

Chase: Tensed running at another individual over a few meters (short chase) or a longer distance (full chase).

Charge: Or charging displays. Tensed running in the direction of, parallel to or closely passing by another individual. Can end up in a clash or other contact aggression.

Bite: "Nipping or cutting into the anatomy of another individual by pressing the teeth on the skin and closing the jaws hard" (Goodall 1968).

Hit: Or punch. Bring down an arm from above and strike another individual with fist or

knuckles.

Kick: Or stamp. Strike or beat another individual forcefully with one foot or both feet.

Clash: Tensed running or swinging in the direction of another individual, resulting in both individuals colliding, and clinging to each other while uttering aggressive screams. Occur more frequently among females.

Push away: “Shove away from another individual with one or both hands...” (Goodall 1968).

Pull: Grasp another individual forcefully with flexing arms.

Attack: A combination of different contact aggressions, e.g., biting and pulling at the same time.

Aggressive signals

Shake branch: Shake branches noisily during agonistic displays directed at humans, monkeys, or conspecifics. May also be performed to solicit copulation.

Arm wave: A threatening gesture. “The arm (whole or forearm only) is raised in a quick jerky movement and the fingers flexed slightly” (Goodall 1968). May also occur in contexts of mating or play to solicit copulation or social play.

Threaten: A gesture or body movement directed at another individual to interrupt his/her behavior or prevent his/her approach. Intention movement or anticipatory gesture of aggression. Examples include: intentional head turn and stare at an individual that is approaching or engaging in a certain social behavior with a third-party individual.

Stand bipedal: Change of body position from sitting/lying down to standing upright on two hind legs. Usually directed at another individual to interrupt or change the behavior he/she is engaging in (e.g., approaching, thrusting, etc.).

Submissive acts

Flee: Running away after a quick aggressive approach, charge, or chase without the indication of play (play face or play vocalization). Lasts at least until the aggressive act

stops.

Jump aside: Leap a few steps (2-3 meters) away from the original spot. Walk away: Or avoid. Locomote away from the aggressor.

Avoidance: Change course of travel direction to keep distance from another individual (who remains still in his/her location).

Give way: Locomote away from the trajectory of movement of another individual so he/she can surpass.

Submissive signal

Pant grunt vocalizations: Observed only in some bonobo populations. In Kokolopori, only observed in subadults. In LuiKotale, observed in adults as well (Schamberg et al. submitted).

1.2 Chacma baboons (*Papio anubis*) at Tsaobis, Namibia

General information

Chacma baboons (*Papio ursinus*) are large, dark, semi-terrestrial primates from the Cercopithecidae family distributed throughout southern Africa. Mean body length is 72 cm for adult males and 61 cm for adult females (Cowlshaw 2013). The species is very sexually dimorphic, with males being twice as heavy as females (mean body mass for adult males: 23-31 kg and adult females: 14-16 kg, Cowlshaw 2013) and harboring much longer canine teeth. Chacma baboons display important ecological flexibility allowing them to inhabit a wide range of habitats, such as desert, savanna and montane grasslands (Fischer et al. 2019). They consume various plant items including fruits, leaves, pods, seeds, bark, subterranean items and flowers, as well as arthropods and small vertebrates that they sometimes kill (Fischer et al. 2019). At night, they sleep on high cliffs or in large trees to be protected from nocturnal predators (Cowlshaw 2013). A given baboon group ranges over the same geographic area over consecutive years, but does not actively defend a territory (Cowlshaw 2013).

Social system

Social organization: Chacma baboons live in large and stable multimale-multifemale groups, comprising typically 20-80 animals. The adult sex ratio is variable within groups, but adult females usually outnumber adult males by 2-3 times (Cowlshaw 2013). Females are philopatric, while males leave their natal group after sexual maturity to immigrate into a new group (Fischer et al. 2019).

Social structure: Males and females establish clear within-sex linear dominance hierarchies, expressed through regular aggressive interactions (threats, chases, physical aggression) and submission signals (Fischer et al. 2019). Adult males dominate all adult females (Kalbitzer et al. 2015). Females generally inherit the rank just below their mother and form matriline (i.e. where maternal sisters occupy adjacent ranks, Fischer et al. 2019). They establish strong, enduring social bonds and alliances with their close kin throughout their life, which positively contribute to their longevity and reproductive success (Silk et al. 2009). Upon dispersal, males fight fiercely to establish and maintain their dominance rank in their new group in order to obtain mating opportunities (Weingrill et al. 2000). Social bonds tend to be strongest between females (Silk et al. 2009), although strong bonds also occur between males and females (Huchard et al. 2010). Inter-group interactions remain frequently peaceful, however resident males can engage in aggressive vocal displays when some females of their group are receptive, and often aggressively chase or “herd” females away from the approaching troop (Kitchen et al. 2005).

Mating system: Females develop perineal swellings during sexual receptivity, that grow in size as they approach ovulation (Huchard et al. 2009). Females are mate-guarded by a high-ranking male when they are likely to conceive (Weingrill et al. 2000). Mate-guarding males maintain close spatial proximity and monopolize sexual access to receptive females. Males also use repeated aggression toward specific females throughout their estrus cycle to encourage their victim to mate with them around ovulation (Baniel et al. 2017). Mate-guarding episodes are long (up to 15 days), and reliably indicate paternity (Weingrill et al. 2000). Male reproductive skew is important and, in consequence, male-male mating competition is high. Infanticide by males account for up to 30% infant mortality in some populations (Cheney et al. 2006). In response, females in early estrus often mate with many males to confuse paternity (Huchard et al. 2009).

Care system: Females give birth every 1-2 years to a single offspring and display prolonged lactation periods (12-13 months, Cowlshaw 2013). Mothers carry their infants ventrally in the first weeks of life, and then dorsally until weaning. During pregnancy and lactation, females generally form tight social bonds with specific males (called “friendships”), that are often the sires of their infants (Huchard et al. 2010). These heterosexual relationships protect offspring against infanticide (Fischer et al. 2019) and translate into preferential male-infant bonds after weaning (Huchard et al. 2013). Dominant males are usually involved in several simultaneous “friendships”, and females associated with the same male compete over access to their male partner, by aggressively displacing subordinate females from his proximity, which contributes to prevent new conceptions with their male friend (Baniel et al. 2018).

Observations

Since 2005, the Tsaobis Baboon Project (<http://tsaobisbaboonproject.org/>) monitors two habituated neighbouring groups of chacma baboons (named L and J) living at Tsaobis Nature Park (22°22'S 15°44'E), Namibia. The study area is a semi-arid rocky savannah located on the edge of the Namib desert along the ephemeral Swakop River. Annual rainfall peaks between January and April, but remains low and variable between years. Each year, a field season of 2-7 months takes place in the austral winter, during which the groups are followed daily on foot from dawn to dusk, to collect detailed demographic, life history, and behavioral data. All individuals are recognizable. Data for this study were collected in June–October 2013 and May–November 2014. Group sizes are as follow: J group (2013, 7–10 males, 17 females, 29–32 juveniles; 2014, 7–8 males, 18 females, 35 juveniles) and L group (2013, 9–11 males, 18–19 females, 31–33 juveniles; 2014, 9 males, 17–19 females, 29 juveniles). Behavioral data were collected using 1h focal observations from all adults. Only affiliative and aggressive interactions between adults were included in the study. For each aggressive act and/or signal emitted by an actor, the reaction of the victim within the two following minutes was extracted, and if occurring, was classified as submissive act(s) and/or signal(s). Males were considered adults when reaching 8 years old and females when they reached menarche. Individual age was estimated from a combination of known birth dates and dental patterns of tooth eruption and wear, examined during prior captures.

Definitions of aggressive and submissive acts and signals

Aggressive acts

Supplant: when one animal actively displaces another to take its place or current resource.

Displacement: when one animal passes close to another and makes it move away (but does not exploit the location/resource previously held by the recipient).

Attack: any agonistic physical contact (including hits, bites, or grabbing movements).

Chase: one animal chases another for a distance of at least 3 m.

Aggressive signals

Gestural threat: a distant gesture/sign of aggression oriented toward the targeted individual. Include staring (eyes are fixed, eyebrows are raised and the scalp is retracted), staring & open mouth (staring accompanied by an open mouth, but with teeth covered), ground sweep (slapping/horizontal sweeping action with one or both hands), head bobbing (head bobs up and down) and pumping cheeks (opening and closing of mouth quickly, while pumping cheeks).

Vocal threat: threat grunt vocalization, with eyes and head oriented toward the recipient (often accompanied with staring and raised eyebrows).

Submissive acts

Run away: one animal runs away from another following an aggressive act or signal.

Walk away: one animal walks away from another following an aggressive act or signal.

Note that a submissive act has been indicated after each displacement, supplant or chase event because these behaviors are defined as eliciting a submissive departure.

Submissive signals

Bare-teeth: recipient shows its teeth as a sign of submission.

Tail-up: the recipient dresses its tail up in the air (usually while running or walking away from the aggressor, and screaming or glancing nervously at him).

Lean away or startle away: the recipient leans away (or bends down towards the ground) or jumps away (at least 1m) from the approaching aggressor. Usually accompanied by a nervous glance at the aggressor and/or bare-teeth.

Fear geck: typical fear scream addressed to the aggressor and usually accompanied with a bare-teeth, while looking intensely at the aggressor.

1.3 Mandrills (*Mandrillus sphinx*) at Lekedi Park, Gabon

General information

Mandrills are forest-dwelling semi-terrestrial Old World primates found in Central Africa (Gabon, Equatorial Guinea, southern Cameroon and Republic of Congo). They are omnivorous with a clear frugivorous tendency, consuming a combination of fruits, seeds, pods, leaves, insects, or small animals (Nsi Akoue et al. 2017). Mandrills are extremely dimorphic with males being ~ 3 times heavier than females (Setchell et al. 2001), displaying 5cm-long upper canines (almost 5 times longer than females, Leigh et al. 2008) as well as extravagant signals in the form of facial and hindquarter colours. Adult males weigh on average 27.5kg and females aged 6 yrs and older weigh on average 9.2kg in the study group (MJEC, pers. Obs.). Mandrills sleep in high trees at night and range over large areas which they do not actively defend.

Social system

Social organization: Mandrills live in multimale multifemale social groups that can consist of several hundreds of members (up to 800; Abernethy et al. 2002). Females are philopatric while males emigrate from their natal group around puberty (Abernethy et al. 2002). They reproduce seasonally with adolescent and adult males immigrating into a new social group, mostly at the beginning of the mating season (May-September; Brockmeyer et al. 2015). Most males leave afterwards but others remain in the social group for variable periods of time (Brockmeyer et al. 2015).

Social structure: Mandrills form typical matrilineal societies with social groups organized around families of maternally-related females. Females establish strong and enduring social bonds with their close kin (Charpentier et al. 2007; 2020). Dominance rank in females is linear and maternally inherited while males compete through fights (Setchell & Wickings 2005) with relatively short and unstable alpha tenures (Charpentier et al. 2005).

Mating system: The mating system of mandrills is polygynandrous. Females display conspicuous sexual swellings around ovulation and males, generally the most dominant, mate-guard females with maximal sexual swellings to monopolize mating access (Setchell et al. 2005). Mate-guarding and paternity success is highly skewed towards the alpha male, with fierce male-male competition during the mating season (Charpentier et al. 2005). Infanticide by males has never been formally observed but is strongly suspected (Dezeure et al. 2022).

Care system: Females give birth to a single offspring every 1-2 years. Mean inter-birth interval is around 20 months in the study mandrills, and shorter for high-ranking females. Infants are typically cared for by their mother, and carried ventrally in their first weeks of life. Average weaning age is 8 months (Dezeure et al. 2022). Males do not provide obvious care to their offspring such as provisioning or carrying but are spatially closer than to any other infants in captivity (Charpentier et al. 2007).

Observations

We studied a group of mandrills ranging in and around the Lekedi Park, near Bakoumba, in Southern Gabon. The group occupies a home range >1,000 ha which exceeds the park's boundaries (Brockmeyer et al. 2015). Other wild mandrill groups live in the area; inter-group encounters are extremely rare but immigrating males regularly join the study group (MJEC pers. obs.). The study area is composed of a mosaic of savannas, grasslands, and evergreen forests. Forested blocks are mainly composed of primary and secondary marantaceae forests with patches of open savannas. The study population of mandrills was established in 2002 after the release in the Lékédi park of 36 (in 2002) and another 29 (in 2006) captive individuals from CIRMF (Peignot et al. 2008). Since 2003 wild males entered the group to reproduce and in 2019, at the time of this study, less than 10 adult fe-

Appendix

males out of ca. 220 individuals were captive-born. This habituated population has been monitored since early 2012 within the framework of the Mandrillus Project. Since 2020, all individuals are individually-recognized and daily monitored. Males are considered as adults around 10 yrs-old and females above 4 yrs-old although they reach their adult size around 7 yrs-old (Setchell et al. 2001). Behavioral data are collected daily through a combination of ad libitum and 5-min focal samplings. In this study, we used data on submissive and agonistic interactions among 72 adults (62 females and 10 males) collected in 2019.

Definitions of agonistic and submissive acts and signals

Aggressive acts:

Grabs or slaps violently: actor grabs or slaps violently recipient

Chase: actor displaces recipient by running at and after recipient

Bite: actor bites recipient

Aggressive signals

Lunge: actor starts chasing recipient but quickly stops a few meters after

Threat by shaking head: actor moves head top to bottom in direction of recipient

Threat by slapping: the ground with the hand: actor slaps the ground with the hand in direction of recipient

Submissive acts

Is displaced by: actor walks away from recipient who takes its spatial position

Avoids: actor walks away from recipient

Runs away from: actor runs away from recipient who expresses aggressive act or signal

Submissive signals

Emits a submissive vocalization: actor emits a submissive vocalization after recipient

expresses aggressive act or signal

Presents hindquarter*: actor presents its hindquarter towards recipient (*Given that "Presents hindquarter" can occur either in a sexual (female mating display) or in a social context (signal of submission), this behavior was taken into account only in the following contexts: (i) in an intra-sexual context and (2) in an inter-sexual context when occurring as a response to agonism).

1.4. Vervet monkeys (*Chlorocebus pygerythrus*) at Inkawu, South Africa

General information

Vervet monkeys are semi-terrestrial omnivore foragers and are widely distributed in sub-Saharan Africa. Mean body length of *Chlorocebus pygerythrus* is 37cm for adult females and 41cm for adult males and mean body mass is 4.1 kg for adult females and 5.7 kg for adult males (Turner et al. 2018). The Inkawu Vervet Project (IVP) is situated in a 12,000-hectares private game reserve: Mawana (28°00.327S, 031°12.348E) in KwaZulu Natal province, South Africa. The vegetation of the study site consisted in a savannah characterized by a mosaic of grasslands and clusters of trees of the typical savannah thornveld, bushveld and thicket patches. Mawana houses various species of animals, including elephants, hippopotamus, giraffes, zebras, and numerous species of antelopes. The common predators of vervet monkeys consist of hyenas, jackals, caracals, servals and several species of snakes and raptors.

Social system

Social organization: Vervet monkeys live in social groups of average size of 25 individuals and up to 76 individuals (Fedigan & Fedigan 1988). They live in multimale multifemale groups comprising, on average, between one and seven adult males and between two and ten adult females and their offspring. Females remain in their natal group while males disperse to a new group when they reach sexual maturity around the age of four. Groups are female-bonded following a matrilineal social organization (Cheney & Seyfarth 1990).

Social structure: Social groups are characterized by a stable linear dominance hierarchy.

Infants generally inherit the rank below their mother in reverse birth order (Cheney & Seyfarth 1990). A higher proportion of males in the group is associated with greater dominance of females over males (Hemelrijk et al. 2020). Vervet monkeys frequently interact with each other. Agonistic interactions occur between conspecifics or during intergroup conflicts in competitive situations to defend access to mates, territory, food, shelter and/or water (Arseneau-Robar et al. 2017). Vervet monkeys also positively interact with each other notably through grooming to strengthen social bonds between individuals (Cheney & Seyfarth 1990). Females form the social core of the group and are the more central individuals in the grooming network (Canteloup et al. 2021). Juvenile males develop relationships with other males by playing with other males, compared to juvenile females who bond with other group members through grooming (Canteloup et al. 2021). Vervet monkeys use three kinds of alarm calls depending on the type of predator: terrestrial predator ('leopard alarm call'), crawling predator ('snake alarm call') and aerial predator ('eagle alarm call'), each eliciting a specific and adapted behavioral response in the recipients (Seyfarth et al. 1980).

Mating system: The mating system is polygynous. All females reproduce giving birth to one infant per year. Males and females present a moderate sexual dimorphism, and the color of males' genitals (red penis and blue scrotum) is a distinguishing characteristic between the two sexes. The breeding season occurs between April and July at IVP. Gestation is approximately 163 days (Andelman et al. 1985) and females give birth to a single infant between September and December. Ovulation is not visually detectable by males (Andelman 1987).

Care system: Females are the ones taking care of infants and males do not provide paternal care for infants.

Observations

In the present study, two groups of vervet monkeys (Noha (NH); Baie Dankie (BD)), have been observed within the IVP. Both groups had been habituated to the presence of human observers since 2010. Observations were made usually between dawn and dusk. In this study, data have been collected over two years for each group; in Noha from 01/01/2013 to 31/12/2013 (NH_2013) and from 01/06/17 to 31/05/18 (NH_2017), and in Baie Dankie from

the 1st January to the 31st of December during both 2016 (BD_2016) and 2018 (BD_2018). In Noha, observers spent 254 days in the field for a total of 1826h in 2013, and 258 days in the field for a total of 1478h in 2017/2018. In Baie Dankie, they spent 261 days for a total of 1074h in 2016, and 237 days for a total of 1883h in 2018. Agonistic interactions have been recorded via *ad libitum* sampling method (Altmann 1974; Martin & Bateson 2021) during natural observations and around food competition tests (i.e., corn provided to the whole groups from a plastic box). During *ad libitum* sampling, observers moved through the group and recorded all social interactions that they observed. IVP observers moved regularly around the group, so they were not always surrounded by the same individuals, avoiding biased data collection. Only dyadic interactions between adults have been taken into account. Polyadic conflicts (i.e. the conflict was redirected to a third individual and/or the victim was supported by other individual) have been removed from the data sample. We considered an individual to have won a conflict if its last behavior in the conflict was aggressive and the last behavior of the opponent was submissive. Males were considered as adults once they dispersed, and females were considered as adults after they gave their first birth. Individuals that did not fulfill these criteria were considered as juveniles. Noha was composed of five adult males and eleven adult females in 2013 and of two adult males and nine adult females in 2017/2018, while Baie Dankie was composed of six adult males and eleven adult females in 2016 and of thirteen adult males and sixteen adult females in 2018. All individuals were identifiable thanks to portrait photographs and specific individual body and face features (scars, colors, shape etc.). Data were collected in part by Charlotte Canteloup and also by different observers from the IVP team. Before beginning data collection, observers had to pass an identification test to ensure correct recognition of all group members as well as an inter-observer reliability test with 80% of reliability for each data category between two observers. Data were collected on handheld computers (Palm Zire 22) using Pendragon software version 5.1 and, at the end of the study, on tablets (Vodacom Smart Tab 2) equipped with the Pendragon version 8.

In previous IVP studies, we entered agonistic interactions in matrix form with the identity of winners in rows and of losers in columns and established dominance with the I&SI method (de Vries 1998) and the Elo-Rating method (Neumann et al. 2011). I&SI method aims to find a rank order most consistent with a linear hierarchy by minimizing the number of inconsistencies and the total strength of inconsistencies. Inconsistencies are dyads

for which the actual dominance relationship does not agree with the relationship in the hierarchy found by the algorithm. While I&SI method uses an interaction matrix organized as a whole to rank individuals, Elo-Rating used the sequence in which interactions occur in time and continuously updates ratings over time. Elo-Rating and I&SI methods have been found to produce very similar dominance rank orders, but Elo-Rating is more powerful in establishing hierarchy when the group size varies and when the proportion of unknown relationships is high (Neumann et al. 2011).

Definitions of agonistic and submissive acts and signals

Aggressive acts:

Hit: the aggressor hits the victim

Bite: the aggressor vigorously bites the victim

Grab: the aggressor vigorously grabs the victim

Attack: the aggressor jumps on the victim

Chase: the aggressor runs after the fleeing victim

Take place: the aggressor takes the victim's place, by displacing the victim which moves away

Steal food: the aggressor takes victim's food

Hand on head: the aggressor puts its hand on the victim's head

Aggressive signals

Stare: an individual visually fixes another one, popping up its white eyelids

Aggressive vocalization: typical aggressive bark emitted by an aggressor towards a victim

Submissive acts

Avoid: the individual changes its trajectory from A to B avoiding the aggressor on its path

Jump aside: an individual jumps aside from the aggressor

Crawl: an individual bows down to an aggressor while looking at it

Leave: an individual walks away from the aggressor

Retreat: an individual quickly leaves the proximity of the aggressor

Flee: an individual runs away from the aggressor

Scream: a short, shrilling vocalization in response to aggression

Submissive signals

Grunt: typical grunting sound when a male approach a higher ranker male

1.5. Crested macaques (*Macaca nigra*) at Tangkoko Reserve, Indonesia

General information

Crested macaques are crested, black, middle-sized primates, expressing important sexual dimorphism: males are typically between 52 and 57 cm from shoulder to rear and weigh about 10kg on average whereas females measure between 44.5 to 57 cm from shoulder to rear and weigh about 5.5kg on average (Rowe & Myers 2017). Crested macaques also exhibit a pronounced canine dimorphism (Marty 2015), as well as sex-biased vocalizations, the males sporting long sharp canines and being the only ones to utter true loud calls in relation to their dominance rank (Neumann et al. 2010). They are endemic to the most northern tip of Sulawesi island in Indonesia and one of the largest known populations lives in Tangkoko Reserve. The Tangkoko Reserve was established in 1980, comprises an area of 8867 hectares, with a sea boundary of 12 km, and ranges from sea level to an elevation of 1350 m. The environment is equatorial, with a mean monthly temperature of 26.4°C (monthly minimum 24.1°C – maximum 28.6°C) and mean monthly rainfall of 122.8mm (range 0 - 365mm) (Macaca Nigra Project data 2006-2021; O'Brien & Kinnaird 1997). There is the equivalent of a dry season between June and September and of a wet season between January and March. The Tangkoko Reserve is mainly covered by secondary regenerating forests, old gardens, and primary rainforests. The

study area is about 500ha, from 0 to 300m above sea level (O'Brien & Kinnaird 1997). Macaques mostly feed on fruits (60 to 70% of their diet) such as from the Anacardiaceae (e.g. *Dracontomelum*) and Moraceae family (e.g. figs) but also eat flowers, leaves, roots, mushrooms, or invertebrates, and, opportunistically, other animals like lizards, snakes or birds (O'Brien & Kinnaird 1997). Aside from humans, their main natural predator is the reticulated python, which they mob if they detect one with alarm calls and branch shaking (Micheletta et al. 2012). Females are considered sexually mature when they can show full sexual swelling and associated sexual behaviors during ovarian cycles while males are considered sexually mature when the scrotum is descended and the canines fully erupted, which we estimated to be between 6 and 8 years old (Macaca Nigra Project data 2006-2021). In the Tangkoko population, pregnancy duration ranges from 171 to 185 days (Kerhoas et al. 2014). Females usually give birth to a single infant on average every 2 years (Macaca Nigra Project data 2006-2021), which they nurse for about a year (Kerhoas et al. 2014). It is unknown if females experience reproductive senescence although it was observed that old females stopped producing babies at some point (Macaca Nigra Project data 2006-2021). In captivity, individuals can live up to 30-35 years; their longevity is unknown in the wild.

Social system

Social organization: Crested macaques live in multimale multifemale multigenerational cohesive social groups, from a dozen individuals to more than a hundred. Female are philopatric and stay in the group they were born in their whole life while males migrate upon reaching sexual maturity, and often change groups several times in their lifetime. As a consequence, crested macaques, like all macaques, are female-philopatric societies presenting a presumably nepotistic hierarchical social structure (Duboscq et al. 2013).

Social structure: Both males and females show a clear dominance hierarchy, with a more or less pronounced steepness (Duboscq et al. 2013; Marty 2015; Tyrrell et al. 2020). The female hierarchy is stable over time and purportedly based on individual and social powers (kin support) whereas the male hierarchy is more unstable at times with shifting power dynamics (Neumann et al. 2011; Duboscq et al. 2013; Marty 2015; Tyrrell et al. 2020). Compared to other macaques, crested macaques are more socially tolerant with frequent friendly body contact between individuals during social interactions, low inten-

sity aggression, high frequency of counter-aggression and reconciliation (Duboscq et al. 2013; Tyrrell et al. 2020). Female grooming networks are dense and diverse indicating that many individuals interact with many others (Duboscq et al. 2013). Kinship and dominance do not strictly structure female social interactions (Duboscq et al. 2017). There is no formal signal of submission in this species as the typical silent bared teeth can be shown to both higher- and lower-ranking individuals and is not linked to a specific agonistic context (Duboscq et al. 2013, Clark et al. 2020). Intergroup encounters are frequent in the study area and can be neutral, positive or aggressive, potentially dependent on the size of the groups, the location of the encounter relative to the core home range of the groups and resource abundance and distribution (Martinez Inigo 2018).

Mating system: Both sex mate promiscuously all year-round and everyone can theoretically reproduce. Females show large sex skin swellings of the anogenital region, which relatively reliably indicate the fertile phase of the ovarian cycle (Higham et al. 2021). Females can reproduce year-round but births exhibit slight seasonal activity, with a majority of infants born from January to May (Kerhoas et al. 2014). In the Tangkoko population, alpha male mating skew during the females' fertile period is about 65% and alpha males are mostly the ones consorting females during their fertile phase with little overlap between females (Higham et al. 2021). As a result, alpha male paternity is rather high, with a mean of 65% of all paternities assigned to the alpha males (range 29-100%, Higham et al. 2021).

Care system: Females are entirely responsible for caring for their young. Depending on their permissiveness, the mother will let other individuals, mostly young females, carry and play with their young baby.

Observations

We studied two groups, PB and R1, comprising about 60 and 80 individuals, respectively. The monkeys were well habituated to human observers, but not provisioned, and spent around 60% of their time on the ground (O'Brien & Kinnaird 1997). We could individually identify all adults based on physical characteristics (shape and color of the anogenital region, wrinkles and special facial features, or scars). The home range of both groups overlapped and included primary forest, secondary forest and old gardens near the village.

During the study periods, R1 had between 18 and 24 adult females and 10-16 adult males and PB had 20 adult females and 8 adult males simultaneously in the group. We followed monkeys on foot from dawn to dusk almost every day and collected data on a hand-held computer on a customized spreadsheet. The data we provide here were collected from October 2008 to April 2010 on 24 focal adult females (2881h observer presence in the group) for R1 and from September 2010 to April 2011 on all adult males and females (418h observer presence in the group) for PB (R1: mean = 60.20h \pm 16.14h SD / individual of focal observation time; PB: 7.72h \pm 0.46h / individual of focal observation time). We carried out focal observations of 30minutes duration where we wrote down the focal individual's main activities (feeding, resting, moving, socializing) every minute and their social interactions continuously. We recorded a total of 4338 agonistic interactions between adult females, between adult males and between males and females, during focal observations and ad libitum, of which 4110 were used in this study (Duboscq et al. 2013; Micheletta et al. 2012).

In previous IVP studies, we entered agonistic interactions in matrix form with the identity of winners in rows and of losers in columns and established dominance with the I&SI method (de Vries 1998) and the Elo-Rating method (Neumann et al. 2011). I&SI method aims to find a rank order most consistent with a linear hierarchy by minimizing the number of inconsistencies and the total strength of inconsistencies. Inconsistencies are dyads for which the actual dominance relationship does not agree with the relationship in the hierarchy found by the algorithm. While I&SI method uses an interaction matrix organized as a whole to rank individuals, Elo-Rating used the sequence in which interactions occur in time and continuously updates ratings over time. Elo-Rating and I&SI methods have been found to produce very similar dominance rank orders, but Elo-Rating is more powerful in establishing hierarchy when the group size varies and when the proportion of unknown relationships is high (Neumann et al. 2011).

Definitions of agonistic and submissive acts and signals

Aggressive acts:

Take over: An individual takes an object that another holds.

Rubbing ground: A forward sliding movement of the hand on a surface.

Lunge/stamp: An individual performs a jump or short run toward another.

Chase: An individual runs after a fleeing individual.

Slap: An individual hits another with the flat of its hand.

Grab: An individual vigorously grabs or pulls another.

Missed hit: A violent movement of the hand toward another that fails to make contact.

Bite: An individual bites another.

Aggressive signals

Staring: A visual fixation on another individual. The scalp may be retracted or not. The head may be thrust forward. The performer is tense.

Half-open mouth: The mouth is slightly open with corners drawn back, the lower lip may be retracted and the teeth are partly visible. This display is accompanied by staring. It is occasionally silent but is most often accompanied by the rattle vocalization.

Open mouth bared-teeth: The mouth is open wide with corners retracted, exposing the teeth and sometimes the gums. This facial expression is accompanied by staring and screaming vocalizations (screams, screeches, chuckles, geckers).

Jaw movement: The head is thrust forward, and the lower jaw is moved up and down rapidly and rhythmically. The mouth is closed or slightly open and the lips slightly protrude. The teeth may be knocked together, and the scalp may be retracted and ears flattened. This expression is accompanied by staring, and may be silent or associated with the hard grunt.

Hard grunt: A plosive grunt containing narrow noise beams. It is accompanied by staring and sometimes jaw movement.

Bark: A loud and brief vocalization that may be repeated, the mouth forming an Oa O shape.

Rattle: A brief and sharp call, usually repeated. It is accompanied by the half-open mouth display

Appendix

Gecker: A tonal sound with frequency modulation, often repeated, accompanied by the open mouth bared-teeth display.

Tonal scream: A long shrill vocalization accompanied by the open mouth bared-teeth display.

Screech: A loud, shrill vocalization accompanied by the open mouth bared-teeth display.

Noisy scream: A shrilling vocalization accompanied by the open mouth bared-teeth display.

Submissive acts

Leave as displaced or supplanted: An individual moves away from an non-threatening but directly approaching individual.

Leave after an agonistic act: An individual moves away from another individual directing an agonistic act or signal towards them.

Crouch: an individual flattens itself to the ground and remains immobile upon another individual directing an agonistic act or signal towards them.

Submissive signals

None known

1.6. Verreaux's sifaka (*Propithecus verreauxi*) at Kirindy Forest, Madagascar

General information

In the present study, data on *Propithecus verreauxi* were collected in Kirindy Forest (44°39'E, 20°03'S), a dry-deciduous forest in the central Menabe region of western Madagascar. The climate of the region consists of a long dry season from April-October followed by a short and hot wet season in November-March with an average annual rainfall of 900mm (Kappeler & Fichtel 2012a). Verreaux's sifaka are a relatively large and monomorphic species of lemur, although females tend to be slightly larger than males (females: 3.69±0.15 kg, males: 3.54±0.86 kg, Kappeler & Fichtel 2012a). They are highly

folivorous, specifically preferring mature leaves and flowers, but also include fruits in their diet (Koch et al. 2017). In Kirindy Forest, infant mortality in the first year is around 55% and mostly due to fosa (*Cryptoprocta ferox*) predation. Individuals reach sexual maturity at around 5 years and can live over 20 years (Kappeler & Fichtel 2012a); in areas with no or little predation up to 30 years Richard et al. 2002.

Social system

Social organization: Sikafa groups at Kirindy are bisexual and contain at least 1 adult-female and 1 adult-male. Group sizes vary from 2-12 individuals with an average of 6 individuals (Kappeler & Fichtel 2012a). Groups can contain up to 3 adult females and up to 3 adult males. Females are philopatric and males disperse at sexual maturity, although females do occasionally transfer voluntarily.

Social structure: Adult female *P. verreauxi* females win all fights against all males in all contexts. Agonistic interactions are infrequent, but clear dominance relationships are discernible within both sexes and dominance hierarchies are moderately steep (e.g. Norscia & Palagi 2015). Both males and females participate in frequent intergroup encounters in peripheral parts of their territories that overlap with those of neighbouring groups (Koch et al. 2016). Scent marking occurs and is done with anogenital or chest glands of dominant adult males (Lewis & van Schaik 2007).

Mating system: The mating system is polygynous. Female *P. verreauxi* enter oestrus for a few days each year, generally asynchronously, resulting in a mating season of about 2 weeks (Mass et al. 2009). The mating season is highly seasonal, ensuring that offspring are born during the time with highest food availability. Gestation takes 6 months and females give birth to one offspring. Interbirth interval is $\sim 15 \pm 5$ months (Kappeler & Fichtel 2012a). Multiple females can give birth in a group, but female-female competition decreases this probability. Reproductive skew is large in this species, with 91% offspring being sired by the dominant male (Kappeler & Schaffler 2008). Females and males reach sexual maturity between 4-5 years. Extra group mating is rare, only observed once in a 15 year study (Kappeler & Fichtel 2012a).

Care system: Maternal investment in offspring is high and, compared to other lemurs, relatively long (weaning at ~ 6 months). Offspring are fully dependent on their mothers for

the first 3 months and are still carried until 6 months (Malalaharivony et al. 2021). Males do not invest much in offspring and have not been shown to exhibit much parental care, but allomaternal care occurs in the form of other females carrying the infant, although this is rare occurring only 2% of the time (Tecot et al. 2013).

Observations

Focal observations of 3 groups of 13 adults (3 females, 10 males) of *P. verreauxi* were conducted between March 2012 and April 2013. Individuals at Kirindy are well habituated to observers and all individuals are equipped with unique nylon collars and pendants for individual identification. One female per group is equipped with a radio-tracked collar to assist in group location in the field. One hour continuous focal observations were done on three individuals per group in the morning (between 07:00 and 11:00h) and afternoon (between 13:30 and 17:30h). Individuals and groups were rotated to ensure that all individuals were observed equally at different times of the day. In total the sifakas were observed for 550 hours for this study, i.e. per individual on average for 42.31 ± 5.46 hours. For dyadic interactions, the ID and the behavior of the partner of the focal animal were recorded.

Definitions of agonistic and submissive acts and signals

Aggressive acts:

Cuff: Actor thrusts body forward and makes contact with receiver

Charge: actor quickly moves entire body towards recipient

Bite: Actor bites recipient

Displacement: Actor approaches another individual, which immediately moves away

Chase: actor displaces recipient by running at and after recipient

Grab: actor grabs part of body or fur of receiver

Wrestle/fight: two individuals “fight” with each other

Aggressive signals

Threat: Actor threatens receiver

Stare: Actor stares aggressively at receiver

Submissive acts

Cower: Individual turns away and makes body smaller or crouches down

Jump away: Individuals jumps away from another, generally following aggression

Flee: Individual moves quickly away from another, generally following aggression

Submissive signals

Chatter call: Vocalization, chattering sounds, occurs immediately following aggression

1.7. Redfronted lemurs (*Eulemur rufifrons*) at Kirindy Forest, Madagascar

General information

The redfronted lemur (*Eulemur rufifrons*, formerly *E. fulvus rufus*) is a cat-sized lemur species with a disjunct distribution in eastern and western Madagascar. Data were collected at the Kirindy Forest field station (44°39'E,20°03'S), a dry-deciduous forest in the central Menabe region of western Madagascar (Kappeler & Fichtel 2012a). This species lives in small multimale multifemale groups of 5-12 individuals that lack pronounced dominance hierarchies. Males and females differ in coloration, but not in size. Females give birth once a year at the end of the dry season to a single offspring. Redfronted lemurs mainly feed on fruits, leaves and flowers, but occasionally include arthropods into their diet (Overdorff 1993). The main predator of redfronted lemurs is the fossa (*Cryptoprocta ferox*).

Social system

Social organization: Groups of redfronted lemurs include on average 9 individuals (5-12), which are composed of 2-3 adult females 3-4 adult males and several immature individuals (Kappeler & Fichtel 2012b). The adult sex ratio is either even or slightly male-biased. The core of the group consists of a few closely related philopatric females, whereas males

disperse after maturation at the age of approximately three years. Females are generally philopatric but are occasionally evicted from groups (Kappeler & Fichtel 2012b). Secondary male dispersal is common, and new males are regularly accepted into groups. Occasionally male take-overs are observed, where one or multiple adult males enter a group and expel some of the original male members of the group (Port et al. 2010).

Social structure: Individuals are usually all socially connected through mutual body contact, as groups often sleep huddled together, e.g., to thermoregulate during cold nights (Ostner et al. 2002). Grooming relationships are more differentiated, with females being socially more central. Dominance relationships are not pronounced (Pereira & Kappeler 1997) and groups are characterized by a high degree of social tolerance (Fichtel et al. 2018). Agonistic interactions are only rarely observed. Communication is mediated by several vocal signals and scents (Pereira & Kappeler 1997; Drea 2020). Intergroup encounters occur mostly in the overlap zone of their home ranges, where groups displace each other by chasing and exhibiting threat displays. During the dry season, intergroup encounters in western populations are more frequent in areas with limited water resources, as groups often travel for kilometers to access them and thereby enter territories of resident groups (Scholz & Kappeler 2004; Scholz and Kappeler 2004). During this time intergroup encounters are more peaceful and multiple groups can be observed resting alongside each other.

Mating system: Redfronted lemurs are plural breeders, and when conditions are good, all females within a group reproduce. The mating period is restricted to a few days as females are in estrus for only 1-2 days each year (Ostner & Heistermann 2003), during which all females copulate with all males, although a single male monopolizes most copulations (Ostner & Kappeler 1999). In groups with a single adult female, one male may monopolize all sired offspring whereas in groups with two or more females, additional males may also reproduce (Kappeler & Port 2008).

Care system: Offspring are almost exclusively cared for by their mothers but are regularly groomed by other group members.

Observations

22 adult individually marked red-fronted lemurs from three groups were observed be-

tween April 2020 and March 2021. Focal animal observations were carried out on all individuals at least 6 times per month, resulting in a total of about 32 observation hours per individual. Focal time was set to 30 minutes per individual, allowing to record most individuals of a group within a session of three hours. Focal observations followed an established ethogram (Pereira & Kappeler 1997). For all agonistic and affiliative interactions, the identity of all individuals involved was recorded. All interactions of the focal individual were recorded using a Psion Teklogix handheld.

Definitions of agonistic and submissive acts and signals

Agonistic interactions involve a total of 19 signals and actions that were defined in Pereira and Kappeler (1997).

Aggressive acts:

Bite: orally seize or slash partner's body part

Hit: Actor hits recipient

Chase: sprint in pursuit of fleeing partner

Body threat: thrust upper torso or whole body toward nearby partner without advancing hindquarters > distance of single leap

Submissive acts

Duck: rapidly lower body or abduct other part away from partner

Flee: run away after gazing at or engaging in non-play interaction

1.8. Rock hyraxes (*Procavia capensis*) at Ein Gedi, Israel

General information

The rock hyrax (*Procavia capensis*) is a diurnal social mammal belonging to the Afrotheria lineage. They are non-selective herbivores with complex digestive systems that allow consumption of poisonous plants. We have been studying six rock hyrax groups at the

Ein Gedi Nature Reserve (31028'N, 35024'E), which is located west of the Dead Sea in the Judean Desert, Israel, since 1999. The reserve comprises two deep gorges, David and Arugot. Adult rock hyraxes in Ein Gedi are dimorphic (mean male weight \pm SD for N = 570 was 2.67 ± 0.45 Kg, while mean female weight \pm SD for N = 733 was 2.3 ± 0.35 Kg). They are seasonal breeders (mating in July–August in our study site) with a long gestation period (approximately 230 days). Females in our study site deliver one to four pups in March, and can live up to 11 years, while the oldest known male reached the age of 9 years .

Social system

Social organization: Rock hyraxes are social, living in stable mixed-sex groups consisting of 3 –20 (average 9 ± 4) females with their pups, 1–2 resident males and late dispersing males (Koren et al. 2006b; Koren & Geffen 2009). Females usually stay with the group, while males disperse between the ages of 16 and 30 months, and often remain in the area near their natal group. Their chance of becoming a resident is about 20%. Resident males are mostly dispersers from outside the research area and remain with a social group for an average of 3.1 years and a maximum of 5 years. Males that do not integrate into a mixed-sex group (i.e., the majority of males), usually remain solitary, as bachelors, or form bachelor groups. Bachelor males may interact with females of several social groups (Koren et al. 2008). Residency status (i.e., resident or bachelor) is not related to body size or social rank, and males that become a resident, remain a resident until they die. Adult longevity (i.e. age at death) is negatively associated with group size, and animals in groups with more equal associations live longer, including resident males, who live longer than bachelors (Barocas et al. 2011). In Ein Gedi, there is an even adult sex ratio.

Social structure: Observations of agonistic interactions suggest female dominance in most groups, which is established by winning aggressive interactions and claiming priority for preferred locations. Testosterone levels are the same in both sexes (Koren et al. 2006b). Although more dominant males have higher testosterone levels than subordinate males, dominant females tend to have lower testosterone levels than more subordinate females (Koren & Geffen, 2009). Agonistic interactions are relatively rare , and most social interactions are affiliative, maintained across years. New individuals that enter the population introduce social instability, which counter the tendency of social relationships to seek a

balance (Ilany et al. 2013). Groups may use overlapping areas but do not socially interact and sleep at different locations than other groups.

Rock hyrax have extensive vocal repertoires, but mostly males engage in singing. Males that sing more are older, more dominant, copulate more, and have higher cortisol levels that are associated with their social status, with dominants having the highest levels (Koren et al. 2008). Songs are composed of 3 elements whose acoustic characteristics, temporal and frequency attributes vary according to the identity of the singer (Koren & Geffen 2011), and are related to singer body weight, size, condition, social status and hormonal state (Koren & Geffen 2009).

Mating system: Rock hyraxes in our study area mate polygynandrously. In the short (1–3 weeks) mating season, both sexes mate with multiple partners, but females are more choosy, rejecting more copulation attempts than males (Ziv et al. 2016). Whereas copulation success increases with the rise in testosterone levels in males, it decreases in females. There is no association between testosterone and choosiness in either sex. However, males with higher testosterone levels mate-guard females with lower testosterone (Koren et al. 2019).

Care system: Mothers nurse offspring for up to a year, but most nursing is in the first 2 months (March and April). All group members, including both resident and bachelor males engage in cooperative social behavior (e.g., babysitting pups and guarding amongst group members (Ziv et al. 2016)). Yet, infanticide by a male has also been observed (Ilany et al. 2011).

Observations

We have been observing rock hyrax social behavior since 1999. Study periods in the field average 6 months a year, from March to August (i.e. parturition until the end of the mating period). Hyraxes are caught using live box traps placed in natural crevices. Trapped animals are anesthetized, weighed, measured, photographed, and individually marked using subcutaneous transponders (DataMars SA, Bedano-Lugano, Switzerland) and a visual identification to facilitate observations. Adults are marked with tagged collars and younger individuals via metal earrings. All measurements are recorded in situ, and the animals are returned to the traps for full recovery, and then released at the capture site.

Animals resumed full normal activity following their release.

We record behavioral observations on social groups using 10 X 42 binoculars and a telescope with X50 and X75 magnifications. Most observations are in the morning from first light to noon, when hyraxes in Ein Gedi retreat to their shelters. All agonistic interactions among individuals are recorded (all occurrences; Altmann 1974), as well as the initiator, recipient and outcome. For the social hierarchy analysis, we considered only agonistic interactions: those that involved display by one individual (i.e. approaching, biting, pushing or chasing) and resulted in an evasive action being taken by a second animal (i.e. running away or retreating from its position).

Definitions of agonistic and submissive acts and signals

Aggressive acts:

Attack: Initiation of aggressive behavior

Fight: aggressive physical interaction

Kill: biting that results in death of another hyrax

Displace: take over the place or position of another individual

Bite: biting another individual

Chase: run after another individual

Threat: Show teeth while approaching another individual

Submissive acts

Flee: run away from another individual

Retreat: receiver's reaction to a displacement

1.9. Spotted hyenas (*Crocuta crocuta*) at Ngorongoro Crater, Tanzania

General information We studied spotted hyenas inhabiting the Ngorongoro Crater, a large caldera with a 250 km² large floor in Northern Tanzania (3°11'S, 35°34'E) characterised by grassland, woodland and swamp vegetation (Anderson & Herlocker 1973). Spotted hyenas are large carnivores; mean body length of Ngorongoro hyenas is 125 cm for adult females and 121 cm for adult males and mean body mass is 56.7 kg for adult females and 51.6 kg for adult males. They are widely distributed in Sub-Saharan Africa, live in a wide range of habitats and hunt a large variety of prey species, ranging from springhares to buffaloes.

Social system

Social organization: Spotted hyenas live in social groups termed 'clans' of up to 130 members. Clans are 'fission-fusion' societies in which members of both sexes often spend time alone or in subgroups of varying size and composition (Davidian et al. 2021). Each clan defends a territory, but individuals frequently intrude into territories of other clans to hunt and scavenge (Höner et al. 2005). Dispersal is strongly male-biased: females typically remain in their birth clan throughout life whereas most males disperse to another clan after reaching sexual maturity (Höner et al. 2005, 2007). Clans therefore usually consist of adult females with their juvenile offspring and three types of adult males: (i) males who are members of their natal clan but have not yet expressed sexual interest in females; (ii) 'philopatric' breeding males who remained in their natal clan and show sexual interest in females of their natal clan; (iii) 'immigrant' breeding males who joined the clan from elsewhere.

Social structure: Clan social structure is characterized by a linear dominance hierarchy. The dominance relationships and clan hierarchy emerge from asymmetries in the number of recruitable social allies between clan members (Vullioud et al. 2019). Social bonds and social support are strongest among close kin and stronger among natives than between natives and immigrants or among immigrants (Smith et al. 2010). As a result, social dominance fluctuates depending on the kin and demographic structure of the clan (Vullioud et al. 2019). Intersexual dominance is usually female biased because in contrast to most males, females remain in their natal clan and retain their network of social allies.

Offspring of both sexes acquire the social rank just below that of their mother through behavioral support and social learning (East et al. 2009) and usually retain the rank below their mother until they die or disperse. Immigrant males start at the bottom of the hierarchy and usually only increase in rank when higher-ranking clan members die or disperse (Davidian et al. 2016). Spotted hyenas frequently interact with each other. Agonistic interactions are most common when they compete over access to large carcasses. These interactions only rarely escalate into physical fights; they are usually resolved by the subordinate individual acting submissively and/or expressing submissive signals (Davidian et al. 2021 and references therein). When two clan members meet, they often also engage in ritualised greetings that function as signs of submission and to reinforce social bonds. Greetings are common among native individuals and among reproductively active (philopatric and immigrant) males but rare between adult females and immigrant males. Spotted hyenas also frequently interact with members of neighbouring clans during clashes over food close to the territorial boundary or when intruding into each other's territories. Dyadic interclan interactions are usually won by the individual closer to the clan's current area of activity and polyadic encounters are won by the clan which recruits the highest number of clan members (Vulllioud et al. 2019).

Mating system: The mating system is polygynandrous. All females reproduce, giving birth to 1 or 2 (very rarely 3) cubs per litter, and there is no distinct breeding season. Females have control over copulation owing to the unusual anatomy of their genitals and exercise mate choice (Höner et al. 2007). Females almost always mate with males of their clan; immigrant and philopatric males are similarly successful (Davidian et al. 2016). There is a considerable degree of reproductive overlap between generations but breeding between close relatives is rare (<1% in Ngorongoro hyenas) because females apply simple, tenure-based mate-choice rules that effectively prevent breeding between daughters and fathers and sisters and older brothers (Höner et al. 2007). Females also frequently chose different sires for subsequent litters, and a substantial proportion of twin and triplet litters (approximately 16% in Ngorongoro hyenas) are sired by more than one father (Höner et al. unpublished data). Reproductive success of both females and males is strongly linked to social rank; high-ranking individuals survive better and produce more offspring than lower ranking individuals, and offspring of high-ranking mothers grow faster, have a higher chance of survival to adulthood, start to reproduce earlier and have

a higher lifetime reproductive success (Hofer & East 2003; Höner et al. 2010; Davidian et al. 2016).

Care system: The females of a clan rear their cubs at a communal den but they typically only nurse their own cubs and adoptions are rare (East et al. 2009). Female investment in cubs is high: the gestation period is 110 days and cubs are nursed for an average of 13 months with highly nutritious milk (Hofer & East 2003). Males do not provide parental care.

Observations

We have been monitoring all spotted hyenas of the eight resident clans of the Ngorongoro Crater since April 1996 (hyena-project.com). Observations are made from a research vehicle to which all hyenas are well habituated, mostly between 06.00 h and 12.00 h in the morning and 16.00 h and 19.00 h in the evening. All hyenas are individually known by their spot pattern and other cues such as ear notches (Höner et al. 2005). Demographic and life-history data are collected routinely during near-daily visits of the study clans. Behavioral data are collected using instantaneous scans as well as all-occurrence and focal animal sampling and usually recorded on video (Davidian et al. 2021). For this study, we used interaction data from adult females and adult males of two clans. Adult hyenas are individuals aged 24 months or older. The age is estimated based on pelage and ear characteristics, body size, behavior, and locomotory abilities and the sex established based on the shape of the phallic glands. Males are considered to be philopatric if they expressed sexual behavior towards females of their natal clan for at least three months (Davidian et al. 2016).

Definitions of agonistic and submissive acts and signals

Aggressive acts:

Bite: actor bites recipient

Stand over: actor stands across recipient

Chin on back: actor lays neck over recipients rump/neck

Sit on top: actor sits on top of recipient

Appendix

Lie down in body contact: actor lies down next to recipient, its body touching that of the recipient

Head move: actor moves head in direction of recipient

Push: actor shoves head into body of recipient

Pull: actor grabs skin of recipient, pulls

Snap: actor jerks head towards recipient without touching it

Lunge: actor quickly moves entire body towards recipient

Chase: actor displaces recipient by running at and after recipient

Wrestle/fight: two individuals “fight” with each other

Approach from broadside: actor approaches recipient and stands in aggressive posture (ears cocked) at 90 degrees, pointing to the side of recipient

Crawl: actor on elbows, teeth bared, ears cocked forward, moving slowly forward

Aggressive signals

Ears forward/cocked: actor draws ears forward with stiff head

Tail horizontal/up: actor moves tail to horizontal position or vertically up

Bare teeth: actor bares teeth (can also be submissive)

Groan: actor expresses quiet, mooing-kind of noise

Submissive acts

Get up: actor gets up on its feet in response to aggressive act or signal by other hyena

Bum down: actor drags bottom over ground to protect it

Side-step/jump: actor moves body and one or several legs away from other individual

Leave/Retreat: actor walks away from hyena expressing aggressive act or signal

Submissive signals

Ears back/flat: ears are drawn back or flat onto the head

Tail down: actor moves tail between hind legs

Head bob: actor throws head up and down rapidly

Head upside down: actor slightly bends in knees and twists head upside down

Mouth open: actor opens mouth and keeps it open

Bare teeth: actor bares teeth (can also be submissive)

Ack: actor expresses strange, rather high-pitched sound

Yell: actor expresses loud, high-pitched, rather short exclamation

Laugh: actor expresses loud, intense, medium-range pitch, with staccato repeats

Yap: actor expresses yap or squeal, less intensive exclamation than yell

Whine: actor expresses quiet, soft, high-pitched exclamation of varying length

Penis/pseudopenis erect: actor erects penis/pseudopenis during greeting

Leg-up: actor lifts leg during greeting

2. Supplementary Figures

		Individual 2			
		A	S	AS	O
Individual 1	A	A-A	A-S	A-AS	A-O
	S	S-A		S-AS	S-O
	AS	AS-A	AS-S	AS-AS	AS-O
	O	O-A	O-S	O-AS	

Figure S1. Possible structures of dyadic agonistic interactions. In a given agonistic interaction, both opponents can either exhibit aggressive (A), submissive (S), both (AS) or no (O) agonistic behavior. Decided interactions, where only one opponent exhibits only submissive behavior (red) can be used to unambiguously determine dominance relationships. Interactions in which only one opponent exhibits aggression (orange) and those where both exhibit aggression and or submission (yellow) or one opponent does not respond to agonistic behavior in kind (purple) lack this unequivocal information and are therefore undecided. It is highly unlikely that both opponents exhibit only submission, and when both fail to exhibit any agonistic behavior, there is no agonistic interaction, so that two theoretical possibilities (white) can be ignored.

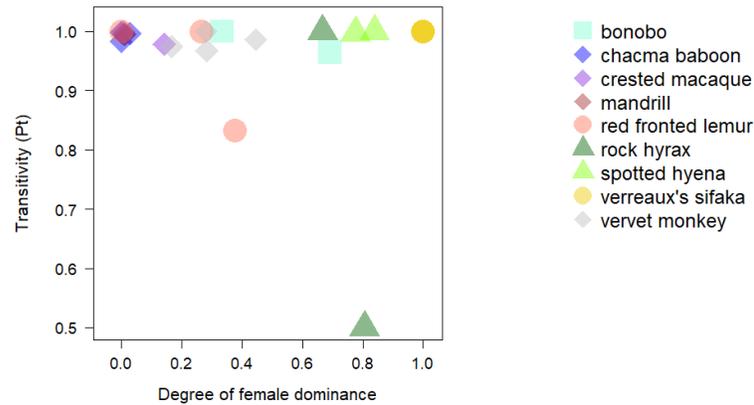


Figure S2: Relationship between the degree of female dominance and transitivity in the different hierarchies. Each data point represents one group-year. The transitivity indices shown here correspond to the intersexual hierarchy with all interactions (occurring both within and among sexes). For consistency with the rest of the manuscript, we used index 1a to measure female dominance.

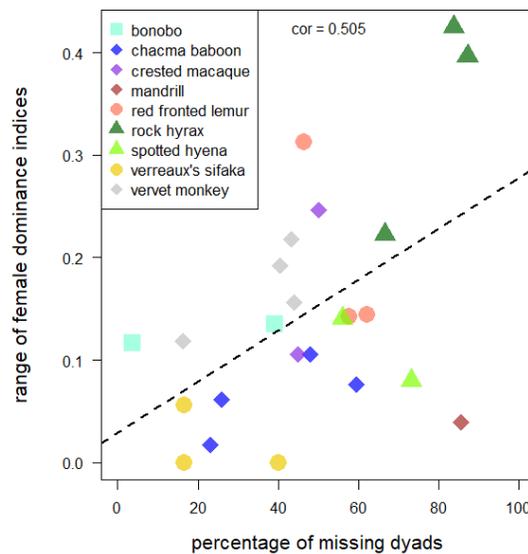


Figure S3: Width of the range of variation in female dominance indices (see figure 2) in relation to the percentage of missing dyads in the datasets. Each species is depicted in a different color. Apes, Old World monkeys, lemurs and non-primate are depicted with squares, diamonds, circles and triangles, respectively.

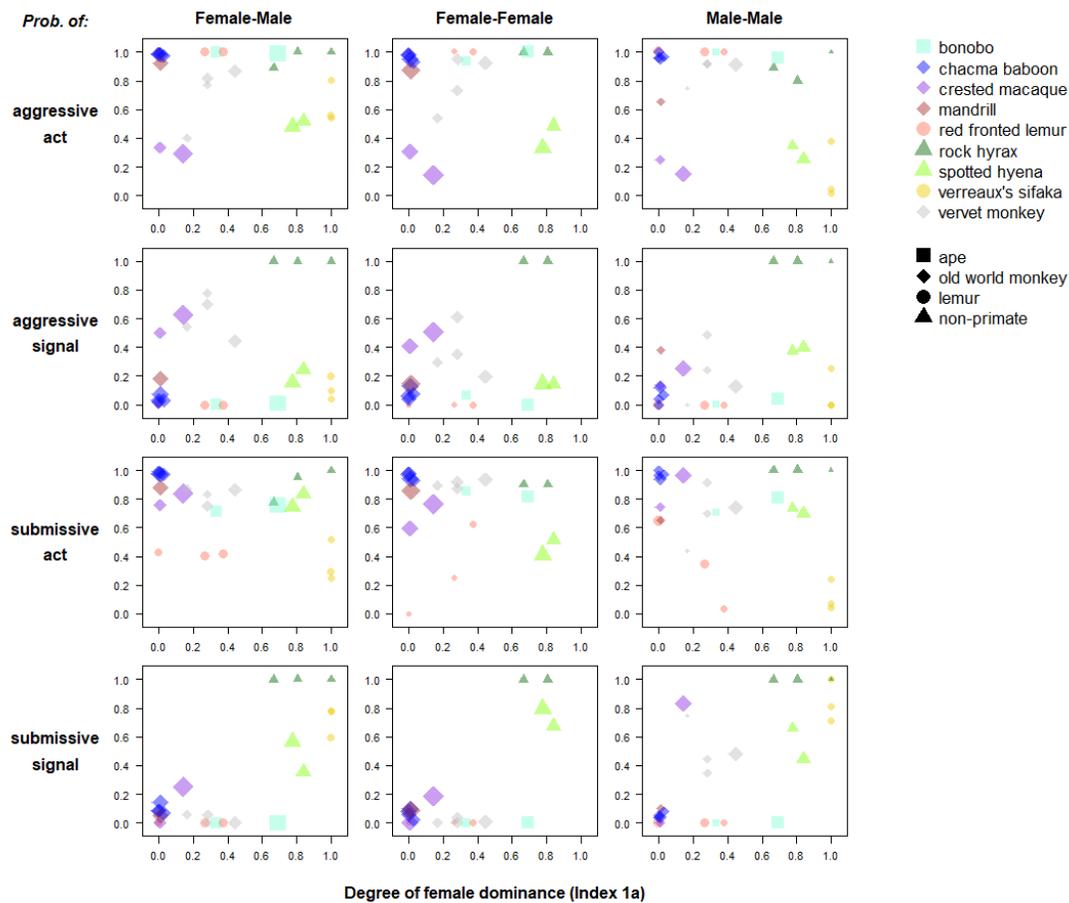


Figure S4: Influence of the degree of female dominance (Index 1a) and dyad type (Female-Male, Female-Female, Male-Male) on the likelihood for conflicts to comprise aggressive acts (top row), aggressive signals (second row), submissive acts (third row) or submissive signals (bottom row). Each dyad type is depicted on a different column (FM on the left, FF in the middle and MM on the right). Each dot represents one dyad type of a study group in a given year, the dot color corresponds to each species (see legend), the dot shape corresponds to larger taxonomic groups (see legend) and the dot size is proportional to the square root of the number of dyads. A square root transformation was chosen here because the number of dyads of each dyad type in the largest groups were several orders of magnitude larger than in the smallest groups.

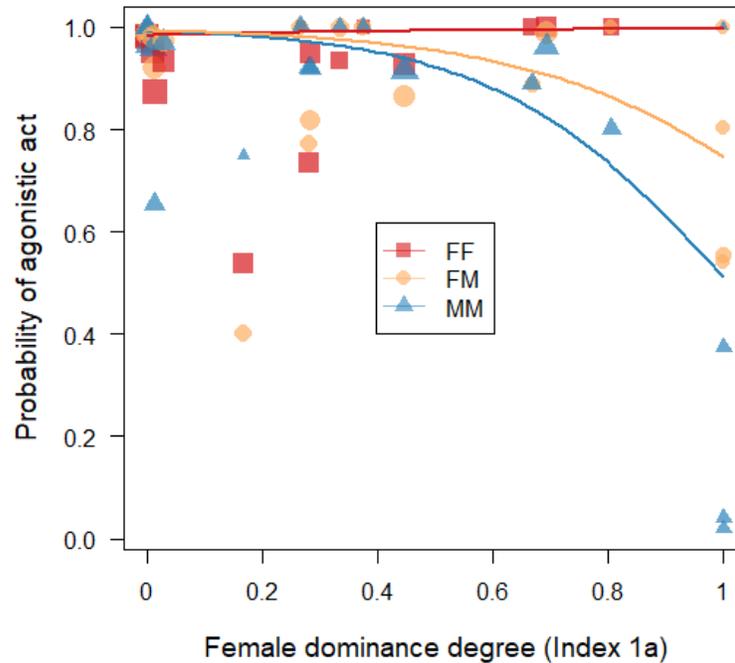


Figure S5: Influence of the degree of female dominance (Index 1a) and dyad type (FM, FF, MM) on the likelihood for conflicts to comprise aggressive acts on a reduced dataset excluding crested macaques and spotted hyenas. Each dyad type is depicted using a different color and symbol: Red square: female-female dyads (FF), orange circle: female-male dyads (FM) and blue triangle: male-male dyads (MM). Each dot represents one dyad type of a study group on a given year and dot size is proportional to the log number of dyads. Log scale was chosen here because the number of dyads of each type in the largest groups were orders of magnitude larger than in smallest groups. The red, orange and blue lines depict the predicted relationship between the degree of female dominance and the likelihood of each act or signal to occur for FF, FM and MM dyads respectively. These lines are derived from Models 2a bis.

3. Supplementary Tables

Table S1: Characteristics of the intersexual hierarchy based only on decided F-M conflicts.

Species	Group	N dyads	Prop. missing dyads	Transitivity (Pt)	Ratio of act vs. signal	Ratio of submissive vs. aggressive behaviors	Prop. of decided conflicts
bonobo	Ekalakala	15	0.00	NA	NA	0.68	0.50
	Kokoalongo	104	0.32	NA	84.67	0.66	0.44
chacma baboon	J_2013	170	0.64	NA	10.73	0.98	0.98
	J_2014	162	0.33	NA	8.49	0.98	0.99
	L_2013	209	0.61	NA	12.92	0.98	0.98
	L_2014	200	0.28	NA	5.88	0.96	0.98
crested macaques	PB	162	0.72	NA	1.97	1.27	0.87
	R1	650	0.52	NA	1.38	1.36	0.83
Mandrills	group 1	620	0.80	NA	4.78	0.91	1.00
red fronted lemurs	B	27	0.56	NA	NA	0.31	0.31
	J	16	0.63	NA	NA	0.44	0.44
	X	16	0.44	NA	NA	0.33	0.33
rock hyrax	Gal	9	0.56	NA	1.00	1.00	1.00
	Isiim	110	0.94	NA	1.00	1.00	1.00
	Suckot	80	0.90	NA	1.00	1.00	0.80
spotted hyena	Lemala	168	0.63	NA	1.51	1.50	0.93
	Munge	208	0.78	NA	1.66	1.66	0.89
verreaux's sifaka	E	3	0.00	NA	0.69	1.50	0.90
	F	3	0.00	NA	1.03	1.05	0.86
	G	4	0.00	NA	0.89	1.31	0.84
vervets	BD_2016	66	0.52	NA	1.36	0.86	0.45
	BD_2018	208	0.65	NA	1.89	0.82	0.69
	NH_2013	55	0.71	NA	1.13	0.86	0.67
	NH_2017	18	0.22	NA	1.94	1.39	0.86

Table S2: Characteristics of the female intrasexual hierarchy (comprising all decided conflicts between females).

Species	Group	N dyads	Prop. missing dyads	Transitivity (Pt)	Ratio of act vs. signal	Ratio of submissive vs. aggressive behaviors	Prop. of decided conflicts
bonobo	Ekalakala	10	0.10	NA	29.00	0.79	0.55
	Kokoalongo	78	0.58	1.00	NA	0.81	0.47
chacma baboon	J_2013	136	0.31	1.00	9.65	0.98	0.98
	J_2014	153	0.15	0.96	6.63	0.97	0.98
	L_2013	171	0.63	0.99	9.62	0.95	0.95
	L_2014	190	0.21	0.99	4.69	0.95	0.96
crested macaques	PB	153	0.29	1.00	1.99	1.06	0.78
	R1	300	0.13	1.00	1.60	1.75	0.81
Mandrills	group 1	1891	0.88	0.99	3.56	1.03	1.00
red fronted lemurs	B	3	0.67	NA	NA	0.40	0.40
	J	1	0.00	NA	NA	0.00	0.00
	X	6	0.50	NA	NA	0.57	0.57
rock hyrax	Gal	3	1.00	NA	NA	NA	NA
	Isiim	45	0.78	1.00	1.00	1.00	1.00
	Suckot	45	0.80	NA	1.00	1.00	0.93
spotted hyena	Lemala	91	0.30	0.99	0.88	1.49	0.90
	Munge	78	0.54	1.00	0.95	1.51	0.81
verreaux's sifaka	E	0	NA	1.00	NA	NA	NA
	F	0	NA	1.00	NA	NA	NA
	G	0	NA	1.00	NA	NA	NA
vervets							

Appendix

Table S3: Characteristics of the male intrasexual hierarchies (comprising all decided conflicts between males). The transitivity index could not be calculated if triads were not present in the interaction matrix (e.g. for all the male-female interaction matrices). For the ratio of acts vs. signals, NA are present when no signal was ever recorded in the dataset.

Species	Group	N dyads	Prop. missing dyads	Transitivity (Pt)	Ratio of act vs. signal	Ratio of submissive vs. aggressive behaviors	Prop. of decided conflicts
bonobo	Ekalakala	3	0.00	1.00	NA	0.83	0.68
	Kokoalongo	28	0.14	1.00	45.00	0.86	0.69
chacma baboon	J_2013	45	0.42	1.00	10.80	1.00	0.96
	J_2014	36	0.39	0.84	15.67	0.97	0.97
	L_2013	55	0.44	1.00	6.50	0.98	0.98
	L_2014	45	0.13	0.95	6.00	0.94	0.93
crested macaques	PB	36	0.42	1.00	14.75	3.19	0.97
	R1	325	0.60	0.88	1.16	3.74	0.97
Mandrills	group 1	45	0.73	1.00	2.00	0.89	1.00
red fronted lemurs	B	36	0.67	NA	NA	0.41	0.41
	J	28	0.57	NA	NA	0.59	0.59
	X	6	0.50	1.00	NA	0.07	0.07
rock hyrax	Gal	3	0.67	1.00	1.00	1.00	1.00
	Isiim	55	0.82	0.00	1.00	1.00	1.00
	Suckot	28	0.71	NA	1.00	1.00	1.00
spotted hyena	Lemala	66	0.76	1.00	0.96	1.45	0.97
	Munge	120	0.77	1.00	1.10	1.56	0.91
verreaux's sifaka	E	3	0.33	NA	0.11	28.00	1.00
	F	3	0.33	NA	0.89	1.50	0.92
	G	6	0.67	NA	0.13	4.00	0.89
vervets							

Table S4: Values of five intersexual dominance indices, per group and species.

Species	Group	Degree of female dominance						
		Index 1a	Index 1b	Index 2a	Index 2b	Index 3	Index 4	Index 5
Bonobo	Ekalakala	0.33	0.40	0.33	0.40	0.38	0.44	0.45
	Kokoalongo	0.69	0.76	0.83	0.80	0.73	0.75	0.79
Chacma baboon	J_2013	0.00	0.00	0.11	0.05	0.00	0.01	0.01
	J_2014	0.00	0.00	0.06	0.04	0.01	0.01	0.01
	L_2013	0.03	0.01	0.09	0.08	0.02	0.03	0.03
	L_2014	0.01	0.01	0.02	0.02	0.00	0.01	0.00
Crested macaque	PB	0.01	0.00	0.25	0.19	0.01	0.01	0.01
	R1	0.14	0.04	0.07	0.10	0.05	0.07	0.05
Mandrill	Group 1	0.01	0.01	0.05	0.03	0.01	0.02	0.02
Redfronted lemur	B	0.27	0.13	0.22	0.22	0.26	0.28	0.21
	J	0.00	0.00	0.13	0.13	0.08	0.06	0.14
	X	0.38	0.31	0.38	0.63	0.44	0.36	0.40
Rock hyrax	Gal	1.00	1.00	0.78	1.00	1.00	1.00	1.00
	Isiim	0.81	0.83	0.57	0.44	0.57	0.76	0.67
	Suckot	0.67	0.60	0.53	0.58	0.24	0.43	0.38
Spotted hyena	Lemala	0.78	0.86	0.76	0.82	0.85	0.87	0.90
	Munge	0.84	0.89	0.87	0.89	0.92	0.88	0.88
Verreaux's sifaka	E	1.00	1.00	1.00	1.00	0.94	0.97	0.94
	F	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	G	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Vervet	BD_2016	0.28	0.20	0.26	0.09	0.24	0.24	0.20
	BD_2018	0.45	0.34	0.39	0.46	0.24	0.35	0.30
	NH_2013	0.28	0.44	0.35	0.44	0.31	0.41	0.40
	NH_2017	0.17	0.17	0.28	0.28	0.16	0.24	0.19

Appendix

Table S5: Effect of the degree of female dominance (Index 1a) on rank differences between intra- and intersexual hierarchies in females (Model 1a) and males (Model 1b). SE indicates the standard error of the estimate for each predictor. § indicates control predictors. CI_{low} and CI_{high} indicate the lower and upper limits of the 95% confidence interval for the estimate of each predictor. The sample sizes for models 1a and 1b are 21 and 24 group_species respectively. Verreaux's sifaka groups were removed from Model 1b since they comprised only 1 female.

Model	Response	Predictor	Est.	SE	CI_{low}	CI_{high}	χ^2	P
1a	Correlation between female intra- and intersexual hierarchies	Intercept	2.08	0.62	0.88	3.37		
		Degree of female dominance	0.15	0.47	-0.93	1.09	0.096	0.756
		<i>% missing female-male dyads</i> §	-0.22	0.14	-0.51	0.05	3.801	0.051
1b	Correlation between male intra- and intersexual hierarchies	Intercept	1.33	0.23	0.95	1.90		
		Degree of female dominance	0.30	0.22	-0.16	0.78	1.613	0.204
		<i>% missing female-male dyads</i> §	-0.19	0.21	-0.68	0.26	0.843	0.359

Table S6: Effect of the degree of female dominance and dyad type (FM, FF, MM) on the probability of using aggressive acts using a reduced dataset excluding data from crested macaques and spotted hyena (Model 2a bis). Since all the continuous variables were standardized to a mean of 0 and a standard deviation of 1, the intercepts and corresponding main effects are indicated for an average degree of female dominance, sex ratio and group size. For all the estimates, female-female dyads are the reference category. SE indicates the standard error of the estimate for each predictor. § indicates control predictors. Significant p-values ($p < 0.05$) are indicated in bold. CI_{low} and CI_{high} indicate the lower and upper limits of the 95% confidence intervals for the estimates of each predictor. The sample size for this model is $N_{\text{interactions}} = 6614$, $N_{\text{dyads}} = 1780$, $N_{\text{individuals}} = 375$.

Response	Predictor	Est.	SE	CI _{low}	CI _{high}	χ^2	P
Did the conflict comprise an aggressive act (Y/N)	Intercept	4.48	0.79	3.10	8.44		
	Dyad type (FM)	-0.27	0.42	-2.19	0.60		
	Dyad type (MM)	-0.55	0.78	-2.84	1.09		
	Degree of female dominance	0.48	0.56	-0.68	3.30		
	Sex ratio [§]	-1.11	0.24	-1.76	-0.42	19.805	0.000
	Group size [§]	0.02	0.29	-0.61	0.63	0.003	0.957
	Female dominance * dyad type (FM)	-1.53	0.43	-4.37	-0.65	14.333	0.001

Appendix 2: Camille, 8 ans: “Pourquoi l’être humain est-il plus évolué que les autres animaux?”

Popular science article published at The Conversation Junior. Nous répondons à la question de Camille, 8 ans, “Pourquoi l’être humain est-il plus évolué que les autres animaux?”. Co-écrit avec Lugdiwine Burtschell, Axelle Delaunay, Jules Dezeure et Elise Huchard.

Tous les organismes présents sur Terre, dont les êtres humains, ne sont pas apparus tels qu’on les connaît aujourd’hui. Leurs formes actuelles sont le résultat de nombreux changements qui se sont accumulés au cours du temps : c’est ce qu’on appelle l’évolution des espèces.

Aujourd’hui, on pense que toutes les espèces descendent d’un unique organisme: on l’appelle LUCA, dont les initiales en anglais veulent dire «dernier ancêtre commun universel». Ce lointain ancêtre aurait vécu il y a environ 3,5 milliards d’années puis ses descendants auraient progressivement donné naissance aux diverses lignées d’organismes que tu connais : les bactéries, les plantes, les animaux, etc. Tu es donc un cousin très éloigné du chêne!

Mais comment une espèce évolue-t-elle ? À la naissance, les individus d’une même espèce ne sont pas tous identiques. Par exemple, imaginons que dans une population de singes, un individu naisse avec une forme de main différente qui lui permette de mieux grimper aux arbres : il pourra mieux se nourrir et s’abriter des prédateurs.

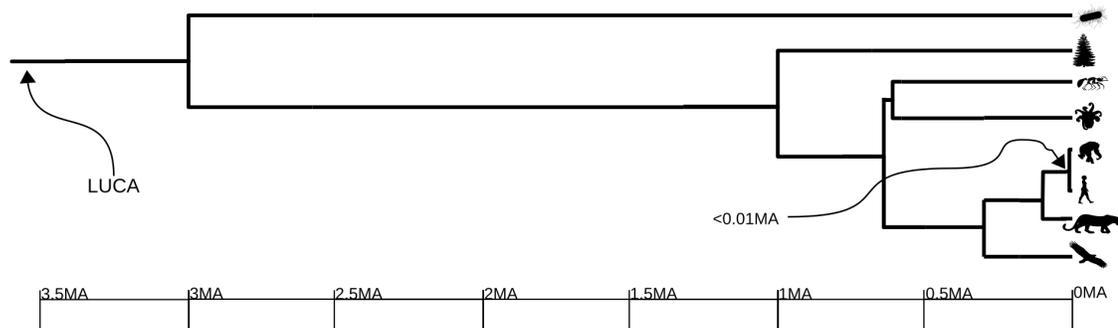


Figure 1: Evolution des espèces actuelles depuis le “Dernier Ancêtre Commun Universel”. MA: Milliards d’années. Silhouettes adaptées d’après Phylopic.

Cette main bizarre lui permettra de vivre plus longtemps, donc d’avoir plus de petits que les autres. Si ses petits héritent de la même main, ils vont eux-mêmes faire plus de petits avec une main bizarre, et ainsi de suite jusqu’à ce que tous les singes de cette forêt possèdent cette «différence».

Cela s’appelle la sélection naturelle, et c’est le moteur de l’évolution. Petit à petit, lorsque deux populations se retrouvent séparées par un obstacle ou une distance infranchissable, de telles différences s’accumulent jusqu’à obtenir deux espèces distinctes.

Peut-on alors dire qu’une espèce est plus évoluée qu’une autre selon les différences qu’elle possède? Non! Le plus souvent, ces différences ne sont des avantages que dans certains environnements. Par exemple, savoir grimper aux arbres est avantageux en forêt, mais pas dans le désert. À force de s’adapter à la grande diversité d’environnements présents sur Terre, les lignées du passé se sont diversifiées en d’innombrables espèces, à l’origine de notre biodiversité. On ne peut donc pas dire qu’une espèce est plus évoluée qu’une autre, seulement qu’elle est mieux adaptée à son environnement.

Les humains seraient-ils donc les meilleurs, car capables de s’adapter à tout type d’environnement? Pas forcément. Par exemple, les fourmis d’Argentine sont aussi présentes presque partout sur Terre, et bien plus nombreuses que nous. C’est sans doute parce que, comme les humains, elles forment des sociétés complexes et ont trouvé des solutions astucieuses : par exemple, elles ont commencé à élever des pucerons des millions d’années avant que les humains ne fassent de même avec les vaches. En effet, elles protègent les

pucerons de prédateurs tels que les coccinelles, et récupèrent en échange leur miellat, une sorte d'eau sucrée dont elles sont très gourmandes. Exactement comme le font les humains avec le lait!

D'autres espèces survivent là où aucun humain ne le pourrait, comme les minuscules tardigrades qui supportent des températures qui vont de -272 à +150 °C, et même le vide spatial!

Mais les humains sont quand même une espèce à part, capable de parler, d'écrire, d'accumuler et de transmettre beaucoup d'information ou encore de construire des fusées : ne sont-ils pas les plus intelligents ? Pas si sûr, car chaque jour, de nouvelles découvertes nous dévoilent d'extraordinaires capacités chez les autres espèces, qui partagent beaucoup des nôtres.

Par exemple, certains chimpanzés sont capables de mémoriser une suite de nombres si rapidement qu'ils battent tous les humains entraînés au même exercice (voir ici). Certains animaux possèdent des cultures, des systèmes de communication très efficaces, une capacité à se projeter dans le futur, ou encore de l'humour ; ils peuvent créer et manier des outils (comme les pieuvres), ressentir des émotions complexes comme la jalousie et le deuil, ou encore faire preuve d'une intelligence remarquable pour manipuler leurs congénères ou résoudre des problèmes complexes (comme les corbeaux).

Une chose est sûre, il est impossible de mesurer si une espèce est « plus évoluée » qu'une autre ! Chaque espèce possède des caractéristiques qui la rendent unique, et il nous reste encore beaucoup à apprendre sur les autres espèces. Qui sait, peut-être que toi aussi, un jour, tu feras des découvertes sur leurs étonnantes capacités?

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Last names are omitted above - to let the identities obscure - in case I change my mind.

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Following the norms, I thank my family - although I didn't choose it - and friends - although occasionally I don't understand why I chose them.

I finally thank maggie and the bands I was listening to, during the thousands of hours in front of this computer.

To those thanksgiven more than once above, belonging to different sets, I take back all my thanksgivings apart from one.

I thank you, because you read this and if you are not anyone from the thanksgiven or a piece of shit, you deserve a dedication - except if you read only this section.

To those I forgot, take some time to think why did this happen - what did you do wrong and you were forgotten.

* Unequal contribution

