The eco-evolutionary landscape of power relationships between males and females

Authors: Eve Davidian[1,*], Martin Surbeck[2], Dieter Lukas[3], Peter M. Kappeler[4,5], Elise Huchard[6,*]

[1] Ngorongoro Hyena Project, Ngorongoro Conservation Area, Arusha, Tanzania; email: davidian.ceve@gmail.com; Twitter: @HyenaProject; ORCID: 0000-0001-9437-0720

[2] Harvard University, Department of Human Evolutionary Biology, Cambridge, MA, USA; email: msurbeck@fas.harvard.edu; ORCID: 0000-0003-2910-2927

[3] Department of Human Behavior, Ecology and Culture, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany; email: dieter_lukas@eva.mpg.de; ORCID: 0000-0002-7141-3545

[4] German Primate Center, Behavioral Ecology Unit, Leibniz Institute of Primate Biology, Göttingen, Germany; email: pkappel@gwdg.de ; ORCID: 0000-0002-4801-487X

[5] University of Göttingen, Department of Sociobiology & Anthropology, Germany

[6] Anthropologie Évolutive, Institut des Sciences de l'Évolution de Montpellier (ISEM), France ; email : elise.huchard@umontpellier.fr; ORCID: 0000-0002-6944-449X

[*] These authors contributed equally

Corresponding authors: Davidian, E. (davidian.ceve@gmail.com), Huchard, E.

(elise.huchard@umontpellier.fr)

Abstract. In mammalian societies, control over resources and reproduction is often biased towards one sex. Yet, the ecological and evolutionary underpinnings of male-female power asymmetries remain poorly understood. We review historical hypotheses and recent empirical data to show that male-female power relationships are more nuanced and flexible than previously acknowledged. We then propose that enhanced reproductive control over when and with whom to mate predicts social empowerment across ecological and evolutionary contexts. We finally outline distinct pathways to sex-biased power: coercion and male-biased dimorphism constitute a co-evolutionary highway to male power, whereas female power emerges through multiple physiological, morphological, behavioural, and socio-ecological pathways. Our framework generates testable predictions regarding the emergence and dynamics of male-female power structures across mammalian social systems.

Keywords: intersexual power inequality; sexual conflicts; social dominance; sexual size dimorphism; reproductive control; social evolution

Highlights

- Inequality in the degree of control (or 'power') that members of one sex exert over members of the other sex is a pervasive characteristic of mammalian societies, including our own.
- The study of the drivers of male-female power relationships has been impeded by methodological and conceptual limitations.
- We propose a comprehensive framework to describe, quantify and predict male-female power relationships within and across species.

- The framework builds on two core principles: (i) power arises from conflicts over reproductive control and social control and (ii) enhanced reproductive control by one sex predicts its social empowerment.
- The framework explains the ecological and evolutionary dynamics of male-female power and why it ranges from strict female to strict male power in mammalian societies.

1. What is power?

Power, defined as the ability to elicit particular behaviours in others [1,2], is a pervasive yet elusive characteristic of social relationships. Identifying the ultimate and proximate underpinnings of power can provide insights into the emergence, dynamics and consequences of social and gender inequalities in human and animal societies; topics of increasing societal significance [3–6]. Power can be divided into two broad domains: ‘resource-holding’ and ‘decisional’ power [7]. Resource-holding power encapsulates the degree of control that one individual can exert over another when competing over resources and mating opportunities [1,2,8]. It emerges through three main non-mutually exclusive mechanisms: (i) **coercion** (see Glossary), where asymmetries in coercive potential may for example arise from differences in intrinsic and social **attributes**, experience, or **motivation** [5], (ii) **deception**, whereby individuals manipulate the information available to others [9], and (iii) **trade**, whereby some individuals may have a bargaining advantage or ‘**leverage**’ because they possess valuable resources and services that can be exchanged (‘commodities’) but cannot be taken by force [1,8,10]. Decisional power, also termed ‘leadership’, commonly refers to the ability of an individual to influence the behaviour of others in ways that generate collective activities in various contexts, such as movement, foraging, hunting, and intergroup conflict [3,4,7]. Asymmetries in resource-holding power between individuals are prevalent in nonhuman mammalian societies and presumably have a deeper and more direct impact on individual survival and reproduction than decisional power [6,11].

In this review, we focus on resource-holding power relationships between males and females (hereafter, "**intersexual power**") in social mammals. Intersexual power determines, and can thus be measured by, whether and how access to resources and reproduction is gained or retained by individuals of one sex [12–15]. Understanding the proximate and ultimate drivers of intersexual power is therefore key for deciphering the eco-evolutionary processes and feedbacks that shape the **social organisation** and **mating system** of mammalian societies.

2. Brief overview of traditional approaches to the study of intersexual power

2.1 The historical hypotheses

Early empirical and theoretical studies of intersexual power have largely focused on the evolutionary drivers of female-biased power [15]. In the centre of attention were a handful of species where females were considered 'masculinised' because they possess behavioural, physiological or morpho-anatomical traits that are more strongly expressed among males in most mammals, such as relatively large body size, high aggressiveness, high levels of androgens, or erectile external genitalia – as in many lemurs [16–18], spotted hyenas (*Crocuta crocuta*) [19], rock hyraxes (*Procavia capensis*) [20], and meerkats (*Suricata suricatta*) [21]. A predominant set of hypotheses has therefore emphasised the role of these intrinsic attributes on female coercive potential [15,18,22]. They posited that females outcompete males when they match or surpass males in size, weaponry or fighting ability.

Extensions of these hypotheses later integrated the role of behavioural and hormonal masculinisation in female empowerment [16,17,19,23]. A second set of hypotheses emphasised asymmetries in motivation that may arise from differences in life history between males and females. They posited that females are more prone to engage in and to win contests with males when they gain higher payoffs than males from accessing resource, e.g., in species where females may incur particularly high reproductive costs [24,25]. A third set of hypotheses highlighted asymmetries in trading ability between the sexes and the role of female leverage through mate choice, whereby females preferentially mate with submissive, deferent or non-coercive males [1,13,26].

2.2. The main conceptual and methodological limitations

These hypotheses and our current understanding of intersexual power have suffered from long-standing stereotypical views of sex roles – as emphasized in pioneering work by women primatologists and anthropologists [e.g., 27,28] – and several other methodological and conceptual limitations [15]. First, previous studies often equated power with coercive social control (also termed 'social dominance') [8,15] that is, control that is acquired and maintained forcefully over resources that are primarily related to an individual's self-maintenance and survival, such as food, shelter, shade or territory; these approaches thereby do not account for (i) alternative, non-coercive mechanisms [8,15] and (ii) the more cryptic, yet key contribution of **reproductive control** [2], and may not fully capture the subtlety and diversity of power relationships between males and females. Second, asymmetries in intersexual power and their causes have rarely been formally tested or quantified by systematically measuring the outcomes of intersexual conflicts. Instead, dominance relationships were, and still are, often studied separately for males and females or only for members of one sex. Species were often categorised as male- or femaledominated based on which sex the sexual dimorphism in size and weaponry was biased towards, or on which sex occupied the top positions in a group's **social hierarchy** [12,14]. Third, male-biased power has often been implicitly considered as the default state, whereas female-biased power has traditionally been viewed as anecdotal and emerging from lineage-specific oddities [19,23], such as the 'lemur syndrome' or the peculiar anatomy of female genitalia in spotted hyenas, moving the topic outside mainstream socio-ecology. These oversimplifications, and the lack of a standardised methodology to quantify intersexual power, have prevented the conceptual integration of intersexual power into the broader evolutionary theories of sexual conflicts and mating systems as well as comparative analyses that could reveal general mechanisms driving biases in intersexual power.

3. Revisiting the landscape of intersexual power

3.1. The fifty shades of intersexual power within and across species

Recent empirical studies that quantified intersexual power in different socio-ecological contexts and in diverse mammalian taxa revealed that intersexual power relationships are much more nuanced and dynamic than previously thought, questioning the long-standing dichotomist views. First, intersexual power is not limited to strict male social dominance (as in Hamadryas baboons *Papio hamadryas* [29]) or strict female social dominance (as in ringed-tailed lemurs, *Lemur catta* [18]) but varies across species along a continuum, including more balanced male-female power – also termed 'co-dominance' or 'egalitarianism' – as in meerkats (*Suricata suricatta*) and vervet monkeys (*Chlorocebus pygerythrus*) [30,31]. Second, intersexual asymmetries in social dominance can exhibit flexibility within a species, as in rock hyraxes [20], European badgers (*Meles meles*) [32], and spotted hyenas [14]. These findings indicate that intersexual power relationships are not necessarily a fixed attribute of a species and are not invariably driven by any particular sex-specific trait. They also call for the broadening of the traditional framework and the study of intersexual power as a dynamic, emergent property of the socio-ecological environment experienced by individuals, groups, populations and species.

3.2. The duality of intersexual power: Reproductive and social control

Here, we outline a unified and comprehensive framework for the study of intersexual power that integrates historical hypotheses and recent empirical and conceptual insights into the broader theories of sexual conflicts and mating system evolution. We synthesise and combine general principles of power with peculiarities of social and mating systems to describe, quantify and predict variations in intersexual power within and across mammalian societies. First, we contend that intersexual power arises from the combined effect of intersexual asymmetries in the degree of (i) control over reproduction and (ii) social control over non-reproductive resources, focusing on five dimensions of power: emergence, generality, durability, payoffs and distribution (Box 1). Second, we propose that the extent of asymmetries in reproductive control between the sexes can be predicted by key features of a species' mating system (Box 2). Third, we argue that intersexual biases in reproductive control play a pivotal role in (i) predicting the empowerment of each sex in the social context and (ii) causing ecological fluctuations and evolutionary shifts in intersexual power.

4. The pathways to male and female reproductive control

Reproductive control has been described as the ability to act in a situation in which conflict over reproduction exists [2,8]. In contexts of sexual conflict, fertilisable eggs can be viewed as a high-value commodity that is owned by females and desired by males [1,8,10]. To acquire this commodity, males try to strategically manipulate the reproductive opportunities and decisions of females, which, in turn, use strategies to resist, evade or discourage male manipulative attempts. This ‘male control-female resistance’ paradigm is at the heart of sexual conflicts over copulation and fertilisation [33,34], which formalises the dynamic power struggles between the sexes over reproductive control.

4.1. Male control pathway

In many mammalian species, sexual dimorphism in size and weaponry is biased towards males, as a result of feedback loops between male-male competition and the mating system (see section 5.1). Striking examples include Hamadryas baboons and elephant seals (*Mirounga angustirostris*) where males can be twice as large and weigh four times more than females, respectively [35,36]. Males often exploit their physical superiority by adopting coercive strategies such as forced copulation, sexual harassment, intimidation or infanticide, which directly increase their mating probability [9,37,38] (Box 2 and Figure 1A). Males may also form alliances, as in bottlenose dolphins (*Tursiops aduncus*), to overcome the difficulty of monopolising females in three-dimensional aquatic environments [39]. Other coercive strategies indirectly increase male mating probability and paternity certainty by preventing females from mating with rivals. For example, pre-copulatory mate-guarding allows males to monopolise access to a sexually receptive female by concurrently restraining female mate choice and aggressively deterring competitors [40,41]. In species with relatively low sexual dimorphism, such as in many rodents, males may deposit copulatory plugs in the reproductive tract of their mating partners as a non-aggressive form of mate-guarding [42]. They may also apply deceptive tactics, as in in territorial ungulates, where males may falsely signal the presence of a predator to discourage females from leaving their territory [9].

4.2. Female resistance pathways

In contrast to males, pathways to female reproductive empowerment are manifold. Females, too, may employ coercion to retaliate against coercive males, either alone or as part of a coalition of females [37] but they may exhibit a wide variety of other behavioural, physiological, morpho-anatomical and life-history traits to resist male sexual coercion (Figure 1A). For example, in some species, females promote male-male competition by advertising their reproductive receptivity, which increases male costs of monopolisation [43]. They may also synchronise sexually receptive periods, which will reduce male incentive to monopolise a given fertile female, because many others are available [34]. Females may alternatively deceive males by displaying unreliable genital swellings or mating outside oestrus [44–46]; such a strategy discourages male attempts to monopolise sexually receptive females and probably played a pivotal role in the evolution of female-biased power in bonobos (*Pan paniscus*) (Box 3). Females may conversely shorten their receptivity period to a few hours per year, as in many lemurs [47,48], a strategy that makes more affordable the considerable energetic costs of resisting male monopolisation attempts [49]. They may also mate sneakily [50] or in locations promoting their reproductive control, as in fossas (*Cyptoprocta ferox*), a non-arboreal carnivore, where females mate in treetops to prevent unwanted mates to climb [51]. To further resist unwanted mating attempts, females may hide their genitals or escape males [9,52], or associate with male allies for protection [53]. In some species, as in many ungulates and bottlenose dolphins, extreme female avoidance of male coercion leads to sexual segregation whereby members of each sex live in distinct (sub)groups for most of the year [54]. Anatomical alteration of the female reproductive tracts may further allow females to gain pre- or post-copulatory reproductive control by either requiring their cooperation for a mating to occur, as in the spotted hyena (Box 1), or by storing sperm from multiple mates and expressing post-copulatory ‘cryptic’ mate choice, as in many bat species [55].

5. How reproductive control promotes social control

Here we propose that the degree of male and female reproductive control determines whether and how members of each sex can empower themselves socially, with respect to access to non-reproductive resources. We further illustrate how the mechanism by which power emerges may influence its durability.

5.1. Coercion: an evolutionary highway to male power

Male coercive reproductive control is facilitated by large male-biased sexual dimorphism in size and weaponry, which is typical of **contest-based** mating systems, and includes all **polygynous** and some **polygynandrous** societies [36,43,56] (Figure 1). In these systems, males often extend their use of coercion to dominate females when competing over non-reproductive resources. Large males may further reinforce intersexual asymmetries in coercive potential and limit female empowerment by controlling their social environment and preventing them from recruiting social allies (Box 2). The tight association between the pervasive use of coercion by males and male-biased sexual dimorphism likely emerges from a co-evolutionary feedback with the mating system (Figure 2). Whenever males gain reproductive payoffs from aggressively monopolising females against competitors, this will (i) promote contest-based competition between males, (ii) subsequently drive the evolution of male-biased sexual dimorphism [36,57], which will (iii) reinforce male coercive potential [35,43]. This will in turn (iv) allow males to gain higher social control and dominance [22,35] and (v) further reinforce their reproductive control over females *via* sexual coercion [35,37,38,43]. Such a potent self-reinforcing pathway may catalyse the emergence and maintenance of male-biased power over evolutionary times, and likely explains why males exert both high reproductive and social control over females in contest-based mating systems (Figure 1), as well as why contest-based systems are widespread among mammals.

A similar coercive co-evolutionary pathway is unlikely to drive female social empowerment because mammalian species in which females concurrently exhibit contest-based intrasexual competition to monopolize access to multiple males and larger body sizes are currently unreported [58,59]. In some species, reproductive competition may be most intense among females; yet, contrary to what would be expected for this co-evolutionary pathway, these species either exhibit sexual monomorphism, as in the polyandrous moustached tamarins (*Saguinus mystax*) [56] and cooperatively-breeding meerkats [30] (Figure 1A), or male-biased size dimorphism as in Damaraland mole-rats (*Fukomis damarensis*) [59]. This apparent paradox probably reflects inherent differences in the life-history and modality of intrasexual competition in females and males [59,60]. Female mammals usually are philopatric and thus predominantly compete with close female kin; they may favour non-coercive forms of competition over direct physical contests with their kin, which fails to select for increased body size and weaponry [59]. This insight emphasises key differences in the pathways to female and male power (Figure 2), in particular that a large body size and overt coercion are not pre-requisites for female empowerment.

5.2. Female social empowerment from leverage based on sex

When females retain some reproductive control, usually in species with moderate sexual size dimorphism as in **monogamous, polyandrous** and **scramble-based polygynandrous** species (Figure 1), they can trade copulations for resources or services that males can provide, such as protection for themselves or their offspring against conspecifics or predators. Yet, such leverage is usually restricted to periods of female sexual receptivity and thereby only confer short-term social empowerment to females – as in some mouse lemurs (*Microcebus spp*.) where female social control over males is more pronounced during the breeding season [61,62]. Leverage-based power may therefore explain female social empowerment over males in species where males are non-permanent residents and join groups only during the mating season, as in rock hyraxes [20]. In species living in permanent groups where males and females maintain long-term, differentiated social relationships, females can extend leverage beyond receptivity periods, if they have enough reproductive control. This strategy may durably promote cooperative behaviour or inhibit aggression from males through mating markets, as in long-tailed macaques (*Macaca fascicularis)* [63] and Guinea baboons (*Papio papio*) [64]. Leverage can then represent a potent source of social control that may, despite male-biased dimorphism, allow females to manipulate the social rank of subordinate males, as in vervet monkeys [65], or to influence male social and competitive relationships, as in bonobos (Box 3). Similar to males, but through a different mechanism, increased social control by females may subsequently reinforce female reproductive control by facilitating their resistance to unwanted solicitations in a positive feedback loop (Figure 2).

5.3. Female social empowerment from mate choice

When female reproductive control enables them to exercise pre-copulatory mate choice, they may select male traits – e.g., social deference, cooperative personalities or a smaller body size – that may, over evolutionary time, increase female social control in a process described by the 'docile male' hypothesis [34]. In bonobos, the related 'self-domestication hypothesis' posits that selection for non-aggressive males, which may partly result from female choice, has contributed to the contrasts in morphology, physiology, behaviour and psychology between male bonobos and chimpanzees (*Pan troglodytes*) [26]. Empirical evidence of female mate choice for such male traits is largely absent in mammals, however [15]. Female preferences for males with whom they are socially-bonded have been reported [66,67], but may reflect leverage rather than choice for male traits that are relevant to intersexual power. Alternatively, female mate choice can promote intersexual power asymmetries indirectly. For example, in spotted hyenas, female reproductive control and mate preferences drive male dispersal [68], which decreases the number of social allies that males can recruit and thus reduces male social control [14].

6. Ecological and evolutionary dynamics in intersexual power

Power relationships between the sexes are closely intertwined with the social organisation and mating system of a species. Positive feedback loops between reproductive and social control suggest that dynamic changes in reproductive control and in the relative payoffs of male and female reproductive strategies are particularly likely to trigger shifts in intersexual power, across both ecological and evolutionary contexts.

6.1 Socio-ecological fluctuations in intersexual power

Wherever power asymmetries between the sexes are moderate, fluctuations in the ecological or social environment – e.g., population density, food abundance, habitat structure, adult sex ratio or kin composition – may cause a change in the social and mating systems, which in turn may affect power relationships between males and females. For example, red foxes (*Vulpes vulpes*) changed their mating system from the typical contest-based polygyny to monogamy [69] following an abrupt decrease in the abundance and quality of prey species caused by an El Niño event, illustrating a shift from male-biased power to a more egalitarian system (Figure 1B). Ecological changes may also alter the relative payoffs of intersexual contests over non-reproductive resources, such as the relative value of one monopolisable food item for male and female reproductive success, therefore affecting the motivation of opponents and the likely outcome of their contest [24]. Fluctuations in the local mating market, for instance due to variation in the adult or operational sex ratio, may affect the extent of leverage possessed by females; e.g., the fewer females are available to mate, the more leverage they have over males [10,70]. This may explain why female power increases with the number of males in the groups of several primate species [12,31]. Conversely, where females have little reproductive control and low leverage as in chimpanzees, sexual coercion by males may instead increase with the number of males in the community, as these dynamics reflect greater male-male competition, and associated male incentive to use coercive strategies [71,72].

6.2 Evolutionary shifts in intersexual power

Male-biased or female-biased power may be evolutionarily stable when reinforced by the positive feedback between reproductive control and social control (Figure 2). This framework predicts a relatively low stability, and thus the relative scarcity, of egalitarian societies where reproductive and/or social control is equally distributed between the sexes. It also predicts the potential for rapid directional evolution towards one or the other end of the intersexual power spectrum, following subtle changes in one keystone component of the system [73,74], which will affect the self-reinforcing evolutionary loop. Factors that reduce the extent of male reproductive control – and reciprocally increase that of females – may thus generate evolutionary shifts in intersexual power within or across species. For example, in the common brushtail possum (*Trichosurus vulpecula*), male sexual dimorphism and degree of polygyny vary in response to different degrees of breeding synchrony in females (influenced by food distribution and seasonality) [75]. Similarly, the emergence of reproductive synchrony in female Kinda baboons (*Papio kindae)* (Box 2) and of deceptive genital swellings in female bonobos (Box 3) have likely contributed to the abrupt shift from male-biased to female-biased power observed in the genera *Papio* and *Pan*, alongside a shift from contest-based to more scramble-based mating systems (Figure 1). Importantly, shifts in intersexual power will probably not occur in isolation but rather follow major transitions in the social organisation and mating system. While sex biases in reproductive control and intersexual power can fluctuate across ecological contexts, broader and more impactful shifts may be expected at an evolutionary scale.

7. Concluding remarks

We break here with the traditional, dichotomist and static view of intersexual power and offer a broader unifying framework that holds a central role for intersexual conflicts over reproductive control. By integrating key concepts of theories of sexual conflict, sexual selection and social evolution, this new framework generates testable predictions regarding the ecological and evolutionary landscape of intersexual power within and across mammalian societies. The scientific investigation of intersexual power is a burgeoning and interdisciplinary research topic where much conceptual and empirical work remains to be done. We hope that this framework will be expanded and stimulate further studies (see Outstanding Questions), notably to develop standardised and widely applicable methods and transdisciplinary tools to quantify intersexual power in reproductive and social contexts and to facilitate the study and comparison of intersexual power relationships across mammalian societies, including humans.

Glossary

Attribute: a trait possessed by an individual at a given time. Intrinsic attributes arise from an individual's physical, physiological or cognitive characteristics; social attributes arise from a relationship to other individuals (e.g., social rank, kinship, number of allies).

Coercion: a strategy to influence the behaviour of others using some form of physical or psychological pressure, which often involves (the threat of) violence and may incur immediate, direct costs or delayed, indirect costs to the target.

Contest-based: a mating system where males aggressively defend reproductive access to multiple females.

Deception: a strategy to influence the behaviour of others that consists of withholding information or sharing inaccurate information to increase uncertainty and promote desired behaviour in other individuals.

Intersexual power: the degree of control over resources and reproduction that members of one sex exert over members of the other sex.

Leverage: a bargaining asymmetry in the control over the modality of an exchange that arises between trading individuals when one possesses a desirable commodity that cannot be taken by force by others (e.g., skills, information, and under certain conditions, fertilisable eggs).

Mating system: the component of a social system that defines the modality of reproduction within a social unit; e.g., the average number of mates of males and females, the strategies applied to access mates, the timing and frequency of matings.

Monogamy: a mating system where a single adult female and a single adult male mate mostly with each other during one or several mating season(s).

Motivation: an incentive to engage in potentially costly behaviours or suboptimal trade to gain or retain access to a resource that is shaped by the (relative) value attributed to the resource and its potential fitness payoff, as determined by the state or life history of the individual.

Polyandry: a mating system where individual females commonly mate with multiple males during a single mating season, whereas males do not mate with more than one female.

Polygynandry: a mating system where males and females both are promiscuous and mate with multiple partners during a mating season.

Polygyny: a mating system where a male can mate with multiple females but each female usually only mates with one male.

Reproductive control: the extent to which an individual can influence the modality of its own reproduction and/or that of others (competitors and potential mates) in terms of the occurrence, timing and frequency of matings and the number and identity of mates.

Scramble-based: a mating system where females cannot be monopolised by males and male-male competition is mostly non-coercive and post-copulatory.

Social hierarchy: the ordinal ranking of individuals belonging to the same social group according to their relative power, typically resource-holding power as derived from the outcome of coercive interactions between pairs of individuals.

Social organisation: a component of a species social system relating to the demographic composition of a social unit.

Trade: an exchange of commodities between individuals. The modality and expected fitness payoff of the exchange are shaped by the local socio-ecological environment.

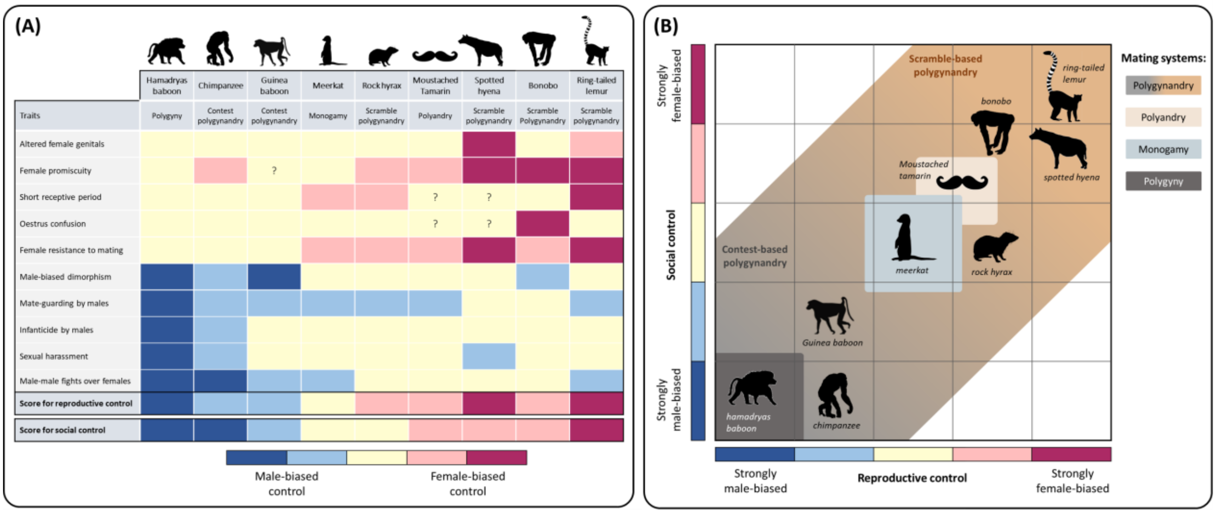

Figure 1. Relationship between mating system, reproductive control and intersexual power. (A) A selection of male and female traits proposed as criteria to quantify male-female biases in reproductive and social control in social mammals as illustrated by nine exemplary species. Colour tones indicate whether the trait promotes or reflects male control (blue), female control (red) or neither (yellow); "?" indicates either missing or non-consensual data in the current literature. Colour darkness reflects the strength of trait expression and, for overall scores of reproductive control and social control, the corresponding degree of intersexual bias. Scores of social control were derived from published indices of social dominance as quantified by the proportions of dyadic agonistic interactions won by males vs. females. **(B)** Putative position of the nine exemplary species (black icons) and their mating systems in relation to intersexual power measured along two axes – reproductive control and social control – as assessed by overall scores in panel A. Coloured areas delineate the proposed range of association between reproductive and social control for four mating systems; polygynandry is represented with a colour gradient to reflect its heterogeneous nature, encompassing species with variable degree of contest-based and scramble-based competition. Intersexual power follows a diagonal from species where power is strongly male-biased in both contexts (see Hamadryas baboons) to strongly

female-biased in both contexts (see ring-tailed lemurs); mammalian societies where reproductive control is strongly female-biased and social control is strongly male-biased, or *vice versa*, are unlikely to emerge. Reference list: Hamadryas baboon [29,45]; chimpanzee and bonobo (see Box 3); Guinea baboon [76] ; meerkat [30,77], moustached tamarin [78–82]; rock hyrax [20,83]; spotted hyena [14,19,84]; ring-tailed lemur [18,48]; cross-specific data [12,35,85]. Credit animal icons: phylopic.org and E. Davidian.

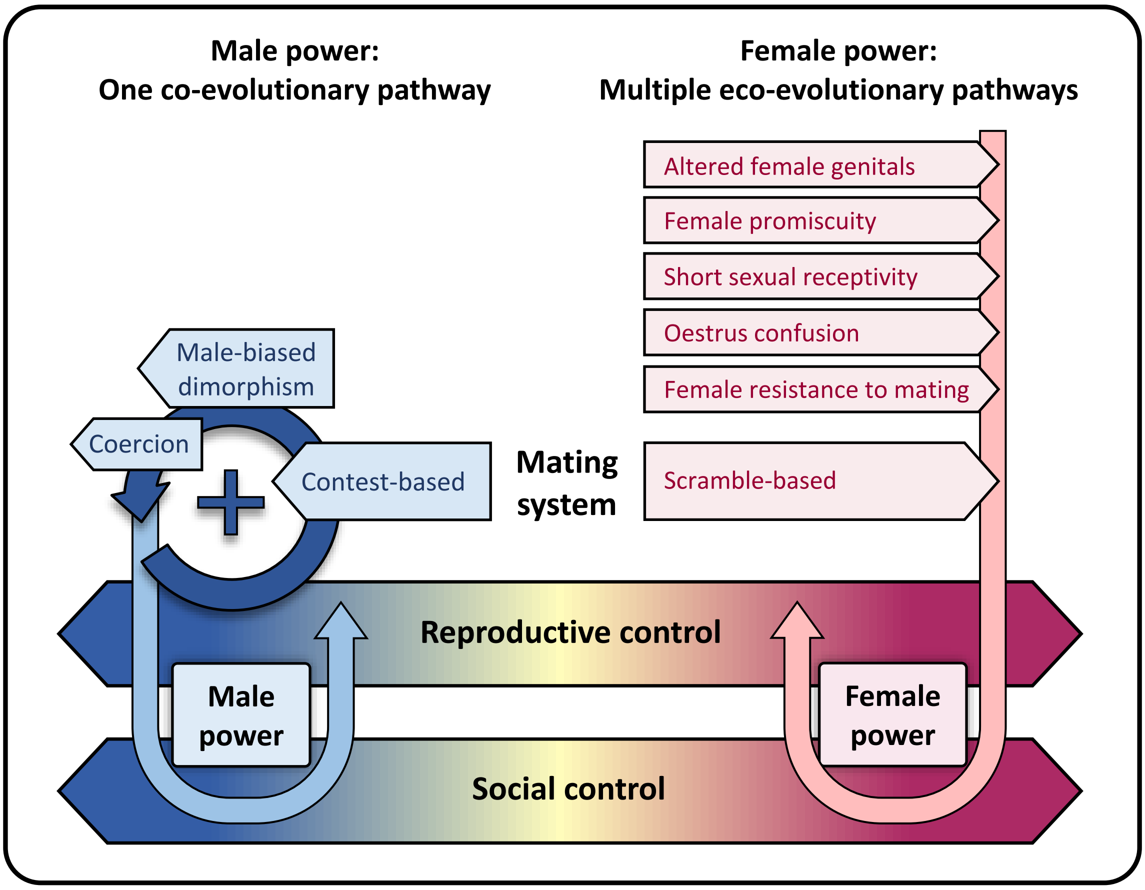

Figure 2. Eco-evolutionary pathways to male and female empowerment in social mammals. This figure summarises the proposed framework to predict intersexual power asymmetries across mammalian societies. It illustrates the interplay and feedback between the mating system and asymmetries in reproductive and social control, and outlines the distinct pathways to male- and female-biased power. Coercion and male-biased dimorphism constitute a co-evolutionary highway to male power in species with contest-based polygyny and polygynandry (left side); Female empowerment emerges through diverse physiological, morphological, behavioural, and socio-ecological pathways (right side) in species with scramble-based polygynandrous, monogamous or polyandrous mating systems.

Box 1. A unified framework for studying intersexual power.

Power can be divided into two non-independent domains, namely resource-holding power and decisional power (or ‘leadership’) [6,7]. We here argue that resource-holding power arises in two main contexts – namely, reproductive and social contexts – defined according to the nature of the resource the two sexes compete over [8] (Figure I). Spotted hyenas nicely illustrate the duality and context-dependence of intersexual power. In this species, females have complete reproductive control owing to the peculiar anatomy of their external genitalia; females lack a vaginal opening (because their labia are fused) and instead possess an elongated and erectile clitoris through which they copulate, urinate and give birth [19]. A direct consequence is that copulation requires the full cooperation of the female and that females can actively choose when and with whom they mate [84]. In contrast, social control in spotted hyenas emerges from asymmetries in the number of recruitable social allies; the extent of intersexual biases in social control may fluctuate between strictly female-biased power structure and balanced social power between males and females, depending on the kin and demographic structure of the group [14]. Building on previous conceptual categorisation of dominance [8], power [86] and leadership [11], we propose that resource-holding power can be described following five dimensions: distribution (extent of asymmetries between the sexes), emergence (whether acquired *via* coercion, deception or trade), durability (stability versus lability), payoffs (sex differences in the fitness benefits to win intersexual contests) and generality (context-dependent or consistency across contexts) (Figure I).

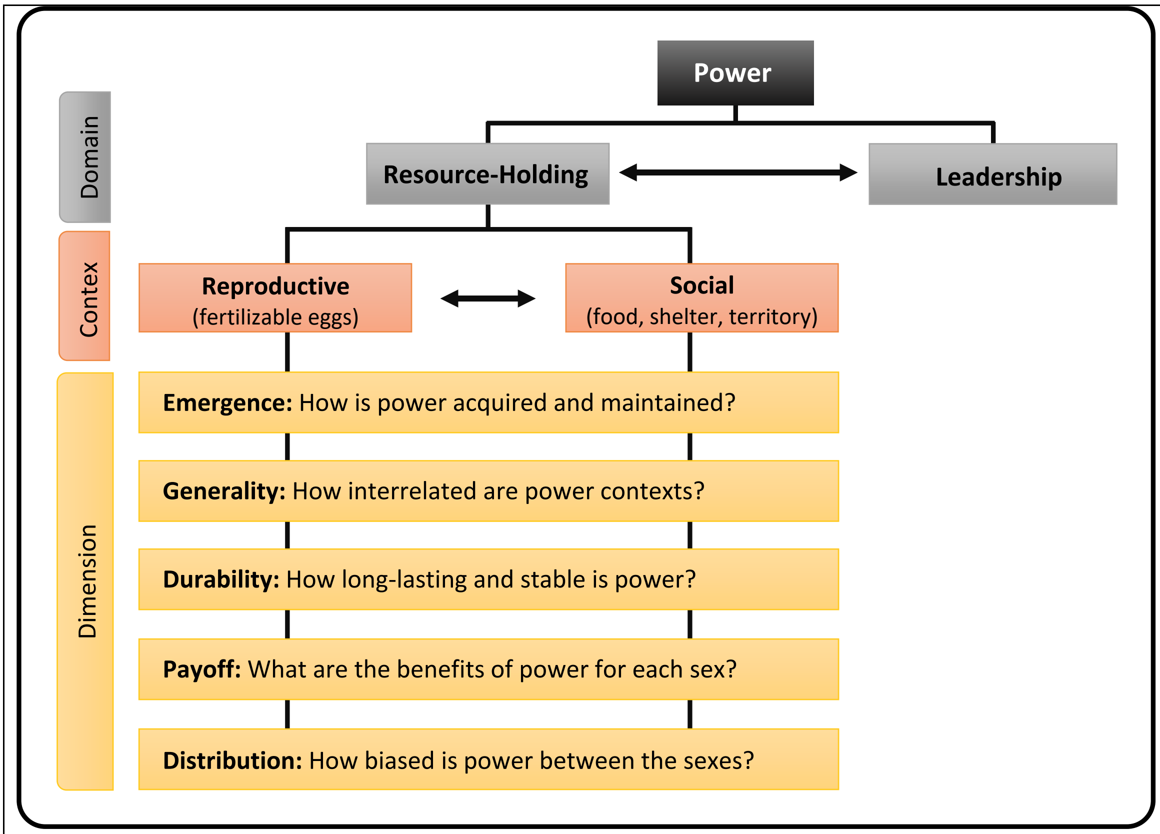

Figure I. Domains, contexts and dimensions of intersexual power. This diagram illustrates the proposed framework to capture the multifaceted nature and the variability of intersexual power in animal societies. Bi-directional arrows indicate the inter-dependence and potential feedback among domains and contexts of power. We here focus on the categorisation of power that emerges from the resource-holding domain.

Box 2. Covariation between male-female asymmetries in reproductive control and mating systems.

Asymmetries in reproductive control between males and females may vary in predictable ways across mating systems. We illustrate such covariation along a gradient across the six baboon species, before generalising (Figure 1). At one end, Hamadryas baboons (*Papio hamadryas*) exhibit contest-based **polygyny** with full male reproductive control; males are much larger than females and maintain harems by forcibly herding females away from their natal group, thereby breaking-up their social ties and support. Harem leaders use various coercive strategies including infanticide after take-overs, and neck-biting when females leave their vicinity [29]. Next, chacma baboons (*P. ursinus*) exhibit predominantly **contest-based polygynandry**. They live in large multimale-multifemale groups with high male reproductive skew – i.e., where access to mates is monopolized by a few males – and intense sexual coercion, including mate-guarding, intimidation and infanticide [87]. Unlike Hamadryas females, chacma females mate promiscuously before ovulation and remain in their natal group; they can form alliances with kin and adult males to seek protection against other coercive males [53]. Next are yellow (*P. cynocephalus*), olive (*P. anubis*) and Guinea baboons (*P. papio*), with a progressive decline in male reproductive skew, sexual dimorphism and coercion, illustrating a decline in the degree of male-biased reproductive control. Guinea males maintain long-term social and sexual bonds with one to two females, females can disperse to other social units and infanticide is unreported [76]. Finally, in Kinda baboons (*P. kindae*), males and females mate promiscuously, male reproductive skew is low and there is no evidence of infanticide [88]. Unlike other species, Kinda baboons breed seasonally and live in very large groups (>200 individuals). These features likely restrict male reproductive control and have likely triggered an evolutionary shift from contest-based to **scramble-based** polygynandry – where male-male competition primarily occurs *via* sperm competition – as suggested by their low sexual dimorphism, relatively large testes and the fact that males queue rather than fight over rank [88]. This gradient illustrates general links between mating system, reproductive control and intersexual power (Figure 1): as male reproductive control weakens, contest-based mating systems are progressively replaced by scramble-based ones, associated with more balanced intersexual power. Where males retain partial reproductive control, but where reproductive competition between females is too high to allow group-living, **monogamy** may initially evolve as a form of permanent mate-guarding [89], decreasing subsequent sexual conflict and paving the way to more equal reproductive control between the sexes and less-coercive mechanisms of intersexual power.

Box 3. Contrasts in female reproductive control and power in our closest living relatives.

Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) live in multimale-multifemale groups in equatorial Africa. In both species, males typically remain in their natal group and females disperse [90]. Their common ancestor likely exhibited male-biased power, as all Great Apes except bonobos [90].

In chimpanzees, adult males dominate adult females and have priority over access to high-value resources like meat [90]. In bonobos, females win most dyadic conflicts against males and enjoy privileged access to meat [13,90,91]. Females in both species exhibit genital swellings when sexually receptive, but bonobo females exhibit longer swollen periods during an interbirth interval [44], despite variation within and between chimpanzee populations in these traits. Consequently, the swellings of bonobo females advertise fertility less reliably than those of female chimpanzees [44,92]. Chimpanzee males can kill infants, are frequently coercive towards receptive females [93], and alpha males have the highest reproductive success, because they can effectively mate-guard females throughout their ovulatory period [94,95]. In contrast, bonobo males do not kill infants, are not sexually coercive and fight less over females, and the high male reproductive skew likely reflects differences in maternal support [96,97].

Following our framework, the initial step towards loss of male-biased power may be the confusion of ovulation, preventing male bonobos from monopolising receptive females and concurrently increasing female reproductive control. This probably reduced the payoff and incentive of males to fight over females, leading to a shift towards scramble-based polygynandry (Figure 1) – as suggested by the relatively larger testes and decreased sexual dimorphism in bonobos compared to chimpanzees [90]. Increased female promiscuity likely further led to the disappearance of male infanticide and sexual coercion. In line with this, male chimpanzees seem more coercive in populations where female fertility signals are shortest (so presumably most reliable) [98]. Female-biased control over resources probably evolved secondarily in relation to their ability to use leverage and exercise mate choice [13,26]. In contrast to males, female bonobos maintain strong bonds, which may be favoured by prolonged sexual receptivity [99,100]; they can form coalitions against males and interfere in male-male competition [90,91,96]. Intersexual differences in female sociality likely reinforced female control over reproduction and resources though whether these are a cause or a consequence of female empowerment remains unclear [90,91,99]. Overall, current evidence is compatible with the scenario that strong contrasts in mating system, intersexual power and social behaviour in chimpanzees and bonobos emerged from subtle changes in female reproductive control.

Outstanding Questions.

Future studies of intersexual power will require the development and standardisation of methods and tools to describe and quantify reproductive and social control (e.g., such as metrics derived from intersexual dominance matrices) across species, mating systems, and ideally also across disciplines, including behavioural ecology, evolutionary biology, economics, sociology, psychology and anthropology. In behavioural ecology, increased effort should be invested in describing under-represented taxa and social systems which have not appeared prominently in the intersexual power literature. As empirical data accumulate, comparative and modelling studies will become central to understand the evolutionary dynamics of intersexual power. We outline key questions that may usefully structure this emerging field.

How should we quantify biases in social control between the sexes? E.g., by the opportunity of each sex to occupy the highest rank(s) in the social hierarchy, by the distribution of sexes across all ranks, or yet using other metrics?

How does intersexual power manifest in species that do not live in permanent mixed-sex groups, such as pair-living, solitary and sexually-segregated species?

How flexible and dynamic are intersexual power relationships across dyads, groups, populations, and species?

How do social organisation and structure interact with the mating system to modulate patterns of intersexual power?

What are the fitness consequences of intersexual power asymmetries and what consequences do they have for group-level traits and demographic processes?

What factors promote ecological and evolutionary shifts in power?

How does the diversity of human societies fit in the spectrum of other mammalian societies and can anthropological and ecological perspectives be integrated?

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