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Eve Davidian, Martin Surbeck, Dieter Lukas, Peter Kappeler, Elise Huchard

► **To cite this version:**

Eve Davidian, Martin Surbeck, Dieter Lukas, Peter Kappeler, Elise Huchard. The eco-evolutionary landscape of power relationships between males and females. *Trends in Ecology & Evolution*, 2022, 37 (8), pp.706 - 718. 10.1016/j.tree.2022.04.004 . hal-03768153

**HAL Id: hal-03768153**

**<https://hal.science/hal-03768153v1>**

Submitted on 2 Sep 2022

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1 **Pre-print.** *This article has been published in Trends in Ecology & Evolution 37 (8), P706-718,*  
2 *August 01, 2022. DOI: <https://doi.org/10.1016/j.tree.2022.04.004>.*

3

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

5

6 **Authors:** Eve Davidian<sup>1,\*</sup>, Martin Surbeck<sup>2</sup>, Dieter Lukas<sup>3</sup>, Peter M. Kappeler<sup>4,5</sup>, Elise  
7 Huchard<sup>6,\*</sup>

8

9 <sup>1</sup> Ngorongoro Hyena Project, Ngorongoro Conservation Area, Arusha, Tanzania; email:  
10 [davidian.ceve@gmail.com](mailto:davidian.ceve@gmail.com); Twitter: @HyenaProject; ORCID: 0000-0001-9437-0720

11 <sup>2</sup> Harvard University, Department of Human Evolutionary Biology, Cambridge, MA, USA;  
12 email: [msurbeck@fas.harvard.edu](mailto:msurbeck@fas.harvard.edu); Twitter: @HarvardHEB; ORCID: 0000-0003-2910-2927

13 <sup>3</sup> Department of Human Behavior, Ecology and Culture, Max Planck Institute for Evolutionary  
14 Anthropology, Leipzig, Germany; email: [dieter\\_lukas@eva.mpg.de](mailto:dieter_lukas@eva.mpg.de); ORCID: 0000-0002-7141-  
15 3545

16 <sup>4</sup> German Primate Center, Behavioral Ecology Unit, Leibniz Institute of Primate Biology,  
17 Göttingen, Germany; email: [pkappel@gwdg.de](mailto:pkappel@gwdg.de) ; ORCID: 0000-0002-4801-487X

18 <sup>5</sup> University of Göttingen, Department of Sociobiology & Anthropology, Germany

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

21 \* These authors contributed equally

22 Corresponding authors: Davidian, E. ([davidian.ceve@gmail.com](mailto:davidian.ceve@gmail.com)), Huchard, E.

23 ([elise.huchard@umontpellier.fr](mailto:elise.huchard@umontpellier.fr))

24 **Abstract.** In animal societies, control over resources and reproduction is often biased  
25 towards one sex. Yet, the ecological and evolutionary underpinnings of male-female power  
26 asymmetries remain poorly understood. We outline a comprehensive framework to quantify  
27 and predict the dynamics of male-female power relationships within and across mammalian  
28 species. We show that male-female power relationships are more nuanced and flexible than  
29 previously acknowledged. We then propose that enhanced reproductive control over when  
30 and with whom to mate predicts social empowerment across ecological and evolutionary  
31 contexts. The framework explains distinct pathways to sex-biased power: coercion and male-  
32 biased dimorphism constitute a co-evolutionary highway to male power, whereas female  
33 power emerges through multiple physiological, morphological, behavioural, and socio-  
34 ecological pathways.

35

36 **Keywords:** intersexual power inequality; sexual conflict; social dominance; sexual size  
37 dimorphism; reproductive control; social evolution

38

### 39 **What is power?**

40 Power, defined as the ability to elicit particular behaviours in others [1,2], is a pervasive yet  
41 elusive characteristic of social relationships. Identifying the ultimate and proximate  
42 underpinnings of power can provide insights into the emergence, dynamics and  
43 consequences of social and gender inequalities in human and animal societies; topics of  
44 increasing societal significance [3–6]. Power can be divided into two main domains:  
45 ‘resource-holding’ and ‘decisional’ power [7]. Resource-holding power encapsulates the  
46 degree of control that one individual can exert over another when competing over resources  
47 and mating opportunities [1,2,8]. It emerges through three main non-mutually exclusive

48 mechanisms: (i) **coercion** (see Glossary), where asymmetries in coercive potential may for  
49 example arise from differences in intrinsic and social **attributes**, experience, or **motivation**  
50 [5], (ii) **deception**, whereby individuals manipulate the information available to others [9],  
51 and (iii) **trade**, whereby some individuals may have a bargaining advantage or '**leverage**'  
52 because they possess valuable resources and services that can be exchanged ('commodities')  
53 but cannot be taken by force [1,8,10]. Decisional power, also termed 'leadership', commonly  
54 refers to the ability of an individual to influence the behaviour of others in ways that  
55 generate collective activities in various contexts, such as movement, foraging, hunting, and  
56 intergroup conflict [3,4,7]. Asymmetries in resource-holding power between individuals of  
57 the same and different sex are prevalent in nonhuman mammalian societies and presumably  
58 have a deeper and more direct impact on individual survival and reproduction than  
59 decisional power [6,11]. These asymmetries may thereby play a key role in shaping the **social**  
60 **organisation** and **mating system** of mammalian societies and will be the focus of this review.

61

## 62 **A novel framework for studying power relationships between males and females**

63 Here we outline a comprehensive framework to describe, quantify and predict ecological  
64 and evolutionary variations in resource-holding power relationships between males and  
65 females (hereafter, "**intersexual power**") within and across mammalian societies. We  
66 introduce three new principles for the framework. First, intersexual power arises from  
67 conflicts over **reproductive control** and social control (Box 1). Second, features of the mating  
68 system predict intersexual biases in reproductive control (Box 2). Third, enhanced  
69 reproductive control by one sex predicts its social empowerment.

70

## 71 **Brief overview of traditional approaches to the study of intersexual power**

72 *The historical hypotheses*

73 Early empirical and theoretical studies of intersexual power have largely focused on the  
74 evolutionary drivers of female-biased power [12]. In the centre of attention were a handful  
75 of species where females were considered ‘masculinised’ because they possess behavioural,  
76 physiological or morpho-anatomical traits that are more strongly expressed among males in  
77 most mammals, such as large body size, aggressiveness, levels of androgens, or erectile  
78 external genitalia – as in many lemurs [13–15], spotted hyenas (*Crocuta crocuta*) [16], rock  
79 hyraxes (*Procavia capensis*) [17], and meerkats (*Suricata suricatta*) [18]. A predominant set  
80 of hypotheses has therefore emphasised the role of intrinsic attributes on female coercive  
81 potential [12,15,19]. They posited that females outcompete males when they match or  
82 surpass males in size, weaponry or fighting ability. Extensions of these hypotheses later  
83 integrated the role of behavioural and hormonal masculinisation in female empowerment  
84 [13,14,16,20]. A second set of hypotheses emphasised asymmetries in motivation that may  
85 arise from differences in life history between males and females. They posited that females  
86 are more prone to engage in and to win contests with males when they gain higher payoffs  
87 than males from accessing resource, e.g., in species where females may incur particularly  
88 high reproductive costs [21,22]. A third set of hypotheses highlighted asymmetries in trading  
89 ability between the sexes and the role of female leverage through mate choice, whereby  
90 females preferentially mate with submissive, deferent or non-coercive males [1,23,24].

91

92 *The main conceptual and methodological limitations*

93 These hypotheses and our current understanding of intersexual power have suffered from  
94 long-standing stereotypical views of sex roles – as emphasized in pioneering work by women  
95 primatologists and anthropologists [e.g., 25,26] – and several other methodological and

96 conceptual limitations [12]. First, previous studies often equated power with coercive social  
97 control (also termed 'social dominance') [8,12] that is, control that is acquired and  
98 maintained forcefully over resources that are primarily related to an individual's self-  
99 maintenance and survival, such as food, shelter, shade or territory. These approaches  
100 thereby do not account for (i) alternative, non-coercive mechanisms [8,12] and (ii) the more  
101 cryptic, yet key contribution of reproductive control [2], and may not fully capture the  
102 subtlety and diversity of power relationships between males and females. Second,  
103 asymmetries in intersexual power and their causes have rarely been formally tested or  
104 quantified by systematically measuring the outcomes of intersexual conflicts. Instead,  
105 dominance relationships were, and still are, often studied separately for males and females  
106 or only for members of one sex. Species were often categorised as male- or female-  
107 dominated based on which sex the sexual dimorphism in size and weaponry was biased  
108 towards, or on which sex occupied the top positions in a group's **social hierarchy** [27,28].  
109 Third, male-biased power has often been implicitly considered as the default state, whereas  
110 female-biased power has traditionally been viewed as anecdotal and emerging from lineage-  
111 specific oddities [16,20], such as the 'lemur syndrome' or the peculiar anatomy of female  
112 genitalia in spotted hyenas, moving the topic outside mainstream socio-ecology. These  
113 oversimplifications, and the lack of a standardised methodology to quantify intersexual  
114 power, have prevented the conceptual integration of intersexual power into the broader  
115 evolutionary theories of sexual conflict and mating systems as well as comparative analyses  
116 that could reveal general mechanisms driving biases in intersexual power.

117

118 **The fifty shades of intersexual power within and across species**

119 Recent empirical studies that quantified intersexual power in different socio-ecological  
120 contexts and in diverse mammalian taxa revealed that intersexual power relationships are  
121 much more nuanced and dynamic than previously thought, questioning the long-standing  
122 dichotomist views. First, intersexual power is not limited to strict male social dominance (as  
123 in Hamadryas baboons *Papio hamadryas* [29]) or strict female social dominance (as in  
124 ringed-tailed lemurs, *Lemur catta* [15]) but varies across species along a continuum,  
125 including more balanced male-female power – also termed ‘co-dominance’ or  
126 ‘egalitarianism’ – as in vervet monkeys (*Chlorocebus pygerythrus*) and meerkats (*Suricata*  
127 *suricatta*) [30–32]. Second, intersexual asymmetries in social dominance can exhibit  
128 flexibility within a species, as in rock hyraxes [17], European badgers (*Meles meles*) [33], and  
129 spotted hyenas [28]. These findings indicate that intersexual power relationships are not  
130 necessarily a fixed attribute of a species and are not invariably driven by any particular sex-  
131 specific trait. They also call for the broadening of the traditional framework and the study of  
132 intersexual power as a dynamic, emergent property of the socio-ecological environment  
133 experienced by individuals, groups, populations and species.

134

### 135 **The distinct pathways to male and female reproductive control**

136 Reproductive control has been described as the ability to act in a situation in which conflict  
137 over reproduction exists [2,8]. In contexts of sexual conflict, fertilisable eggs can be viewed  
138 as a high-value commodity that is owned by females and desired by males [1,8,10]. To  
139 acquire this commodity, males try to strategically manipulate the reproductive opportunities  
140 and decisions of females, which, in turn, use strategies to resist, evade or discourage male  
141 manipulative attempts. This ‘male control-female resistance’ paradigm is at the heart of  
142 sexual conflict over copulation and fertilisation [34,35], which formalises the dynamic power

143 struggles between the sexes over reproductive control. Whether and to what extent  
144 reproductive control is biased between the sexes is largely predicted by key features of the  
145 mating system (Box 2 and Figure 1A).

146

#### 147 *Male control pathway*

148 In many mammalian species, sexual dimorphism in size and weaponry is biased towards  
149 males. Striking examples include Hamadryas baboons and elephant seals (*Mirounga*  
150 *angustirostris*) where males can be twice as large and weigh four times as much as females,  
151 respectively [36,37]. Males often exploit their physical superiority by adopting coercive  
152 strategies such as forced copulation, sexual harassment, intimidation or infanticide, which  
153 directly increase their mating probability [9,38,39] (Box 2 and Figure 1A). Males may also  
154 form alliances, as in bottlenose dolphins (*Tursiops aduncus*), to overcome the difficulty of  
155 monopolising females in three-dimensional aquatic environments [40]. Other coercive  
156 strategies indirectly increase male mating probability and paternity certainty by preventing  
157 females from mating with rivals. For example, pre-copulatory mate-guarding allows males to  
158 monopolise access to a sexually receptive female by concurrently restraining female mate  
159 choice and aggressively deterring competitors [41,42]. In species with relatively low sexual  
160 dimorphism, such as in many rodents, males may deposit copulatory plugs in the  
161 reproductive tract of their mating partners as a non-aggressive form of mate-guarding [43].  
162 They may also apply deceptive tactics, as in territorial ungulates, where males may falsely  
163 signal the presence of a predator to discourage females from leaving their territory [9].

164

#### 165 *4.2. Female resistance pathways*



166 In contrast to males, pathways to female reproductive empowerment are manifold.  
167 Females, too, may employ coercion to retaliate against coercive males, either alone or as  
168 part of a coalition of females [38] but they may exhibit a wide variety of other behavioural,  
169 physiological, morpho-anatomical and life-history traits to resist male reproductive control  
170 (Figure 1A). Females may promote male-male competition by advertising their reproductive  
171 receptivity, which increases male costs of monopolisation [44]. They may also synchronise  
172 sexually receptive periods, which will reduce male incentive to monopolise a given fertile  
173 female, because many others are available [35]. Females may alternatively deceive males by  
174 displaying unreliable genital swellings or mating outside oestrus [45–47]; such a strategy  
175 discourages male attempts to monopolise sexually receptive females and probably played a  
176 pivotal role in the evolution of female-biased power in bonobos (*Pan paniscus*) (Box 3).  
177 Females may conversely shorten their receptivity period to a few hours per year, as in many  
178 lemurs [48,49], a strategy that makes the considerable energetic costs of resisting male  
179 monopolisation attempts more affordable [50]. They may also mate sneakily [51] or in  
180 locations promoting their reproductive control. For example, in fossas (*Cytoprocta ferox*), a  
181 non-arboreal carnivore, females mate in treetops, a location that facilitates their filtering of  
182 candidate males that queue on the ground, by letting preferred males climb and pushing the  
183 others back down [52]. To resist unwanted mating attempts, females may also hide their  
184 genitals, escape males [9,53], or associate with male allies for protection [54]. In banded  
185 mongooses (*Mungos mungo*), females incite intergroup conflicts to escape mate-guarding by  
186 males of their group and mate with extra-group males in the mist of the battle [55]. In some  
187 species, as in many ungulates and bottlenose dolphins, extreme female avoidance of male  
188 coercion leads to sexual segregation whereby members of each sex live in distinct  
189 (sub)groups for most of the year [56]. Anatomical alteration of the female reproductive tract

190 may further allow females to gain pre- or post-copulatory reproductive control by either  
191 requiring their cooperation for a mating to occur, as in the spotted hyena (Box 1), or by  
192 storing sperm from multiple mates and expressing post-copulatory 'cryptic' mate choice, as  
193 in many bat species [57].

194

## 195 **How reproductive control promotes social control**

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

200

### 201 *Coercion: an evolutionary highway to male power*

202 Male coercive reproductive control is facilitated by large male-biased sexual dimorphism in  
203 size and weaponry, which is typical of **contest-based** mating systems, and includes most  
204 **polygynous** and some **polygynandrous** societies [37,44,58] (Figure 1). In these systems,  
205 males often extend their use of coercion to dominate females when competing over non-  
206 reproductive resources. Large males may further reinforce intersexual asymmetries in  
207 coercive potential and limit female empowerment by controlling their social environment  
208 and preventing them from recruiting social allies (Box 2). The tight association between the  
209 pervasive use of coercion by males and male-biased sexual dimorphism likely emerges from  
210 a co-evolutionary feedback with the mating system (Figure 2). When males gain  
211 reproductive payoffs from aggressively monopolising females against competitors, this will  
212 often (i) promote contest-based competition between males, (ii) subsequently drive the  
213 evolution of male-biased sexual dimorphism [36,37], which will (iii) promote male coercive

214 reproductive control over females, and (iv) drive male social empowerment and dominance  
215 over females [19,36,44]. This will (v) ultimately close the loop by strengthening male  
216 reproductive control over females [38,39,44,58]. When female resistance strategies fail to  
217 prevent or disrupt this potent self-reinforcing loop, it may catalyse the emergence and  
218 maintenance of male-biased power over evolutionary times. This likely explains why males  
219 often exert both high reproductive and social control over females in contest-based mating  
220 systems (Figure 1), and why contest-based systems are widespread among mammals. In  
221 addition, female strategies may sometimes reinforce rather than disrupt the loop favouring  
222 male power. For example, where males already have high reproductive control and females  
223 cannot mate promiscuously to dilute paternity, they may instead concentrate paternity to  
224 seek paternal protection in response to infanticidal threats [59]. Such paternity  
225 concentration strategies may contribute to locking females into male-dominated societies.

226

#### 227 *Why the coercive pathway is not the females' way*

228 A similar coercive co-evolutionary pathway is unlikely to drive female social empowerment  
229 because mammalian species in which females concurrently exhibit contest-based intrasexual  
230 competition to monopolize access to multiple males and larger body sizes are currently  
231 unreported [60,61]. In some species, reproductive competition may be most intense among  
232 females; yet, contrary to what would be expected for this co-evolutionary pathway, these  
233 species either exhibit sexual monomorphism, as in the polyandrous moustached tamarins  
234 (*Saguinus mystax*) [58] and cooperatively-breeding meerkats [30] (Figure 1A), or male-biased  
235 size dimorphism as in Damaraland mole-rats (*Fukomis damarensis*) [61]. This apparent  
236 paradox probably reflects inherent differences in the life-history and modality of intrasexual  
237 competition in females and males [61]. Female mammals often compete using subtle forms

238 of coercion – e.g., using threats and agonistic signals – which do not select for increased  
239 body size and weaponry. There are at least three reasons for this: first, theory predicts  
240 avoidance of overt aggression for the sex that faces highest costs of offspring production  
241 [62]; second, the incentive for females to engage in physical contest may be low because  
242 sharing resources is often less costly for females than for males; third, mammalian females  
243 are usually philopatric and thus predominantly compete with close female kin, with whom  
244 they may avoid engaging in costly contests [61]. These insights emphasise key differences in  
245 the pathways to female and male power (Figure 2), in particular that a large body size and  
246 overt coercion are not pre-requisites for female empowerment.

247

#### 248 *Female social empowerment from leverage based on sex*

249 When females retain some reproductive control – usually in species with moderate sexual  
250 size dimorphism as in **monogamous**, **polyandrous** and **scramble-based polygynandrous**  
251 species (Figure 1) – they can trade copulations for resources or services that males can  
252 provide, such as protection for themselves or their offspring against conspecifics or  
253 predators. Yet, such leverage is usually restricted to periods of female sexual receptivity and  
254 thereby only confer short-term social empowerment to females, as in some mouse lemurs  
255 (*Microcebus spp.*) where female social control over males is more pronounced during the  
256 breeding season [63,64]. Leverage-based power may therefore explain female social  
257 empowerment over males in species where males are non-permanent residents and join  
258 groups only during the mating season, as in rock hyraxes [17]. In species living in permanent  
259 groups where males and females maintain long-term, differentiated social relationships,  
260 females can extend their leverage beyond the receptive period. This strategy may durably  
261 promote cooperative behaviour or inhibit aggression from males through mating markets, as

262 in long-tailed macaques (*Macaca fascicularis*) [65] and Guinea baboons (*Papio papio*) [66].  
263 Leverage can then represent a potent source of social control that may, even under male-  
264 biased dimorphism, allow females to manipulate the social rank of subordinate males, as in  
265 vervet monkeys [32], or to influence male social and competitive relationships, as in  
266 bonobos (Box 3). Similar to males, but through a different mechanism, increased social  
267 control by females may subsequently reinforce female reproductive control by facilitating  
268 their resistance to unwanted solicitations in a positive feedback loop (Figure 2).

269

#### 270 *Female social empowerment from mate choice*

271 When female reproductive control enables them to exercise pre-copulatory mate choice,  
272 they may select male traits – e.g., social deference, cooperative personalities or a smaller  
273 body size – that may, over evolutionary time, increase female social control in a process  
274 described by the ‘docile male’ hypothesis [35]. In bonobos, the related ‘self-domestication’  
275 hypothesis posits that selection for non-aggressive males, which may partly result from  
276 female choice, has contributed to the contrasts in morphology, physiology, behaviour and  
277 cognition between male bonobos and chimpanzees (*Pan troglodytes*) [24]. Empirical  
278 evidence of female mate choice for such male traits is scarce in mammals, however [12].  
279 Female preferences for males with whom they are socially-bonded have been reported  
280 [67,68], but may reflect leverage rather than choice for male traits that are relevant to  
281 intersexual power. Alternatively, female mate choice can promote intersexual power  
282 asymmetries indirectly. For example, in spotted hyenas, female reproductive control and  
283 mate preferences drive male dispersal [69], which decreases the number of social allies that  
284 males can recruit and thus reduces male social control [28].

285

286 **Ecological and evolutionary dynamics in intersexual power**

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

292

293 *Socio-ecological fluctuations in intersexual power*

294 Wherever power asymmetries between the sexes are moderate, fluctuations in the  
295 ecological or social environment – e.g., population density, food abundance, habitat  
296 structure, adult sex ratio or kin composition – may cause a change in the social and mating  
297 systems, which in turn may affect power relationships between males and females. For  
298 example, red foxes (*Vulpes vulpes*) changed their mating system from the typical contest-  
299 based polygyny to monogamy [70] following an abrupt decrease in the abundance and  
300 quality of prey species caused by an El Niño event, illustrating a shift from male-biased  
301 power to a more egalitarian system (Figure 1B). Ecological changes may also alter the  
302 relative payoffs of intersexual contests over non-reproductive resources, such as the relative  
303 value of one monopolisable food item for male and female reproductive success, therefore  
304 affecting the motivation of opponents and the likely outcome of their contest [21].

305 Fluctuations in the local mating market, for instance due to variation in the adult or  
306 operational sex ratio, may affect the extent of leverage possessed by females; e.g., the fewer  
307 females are available to mate, the more leverage they have over males [10,71]. This may  
308 explain why female power increases with the number of male group members in several  
309 primate species [27,31]. Conversely, where females have little reproductive control and low

310 leverage as in chimpanzees, sexual coercion by males may instead increase with the number  
311 of males in the community, as these dynamics reflect greater male-male competition, and  
312 associated male incentive to use coercive strategies [72,73].

313

#### 314 *Evolutionary shifts in intersexual power*

315 Male-biased or female-biased power may be evolutionarily stable when reinforced by the  
316 positive feedback between reproductive control and social control (Figure 2). This  
317 framework predicts a relatively low stability, and thus the relative scarcity, of egalitarian  
318 societies where reproductive and/or social control is equally distributed between the sexes.  
319 It also predicts the potential for rapid directional evolution towards one or the other end of  
320 the intersexual power spectrum, following subtle changes in one keystone component of the  
321 system [74,75], which will affect the self-reinforcing evolutionary loop. Factors that reduce  
322 the extent of male reproductive control – and reciprocally increase that of females – may  
323 thus generate evolutionary shifts in intersexual power within or across species. For example,  
324 in the common brushtail possum (*Trichosurus vulpecula*), male sexual dimorphism and  
325 degree of polygyny vary in response to different degrees of breeding synchrony in females  
326 (influenced by food distribution and seasonality) [76]. Similarly, the emergence of  
327 reproductive synchrony in female Kinda baboons (*Papio kindae*) (Box 2) and of deceptive  
328 genital swellings in female bonobos (Box 3) have likely contributed to the abrupt shift from  
329 male-biased to female-biased power observed in the genera *Papio* and *Pan*, alongside a shift  
330 from contest-based to more scramble-based mating systems (Figure 1). Importantly, shifts in  
331 intersexual power will probably not occur in isolation but rather follow major transitions in  
332 the social organisation and mating system. While sex biases in reproductive control and

333 intersexual power can fluctuate across ecological contexts, broader and more impactful  
334 shifts may be expected at an evolutionary scale.

335

### 336 **Concluding remarks**

337 We break here with the traditional, dichotomist and static view of intersexual power and  
338 offer a broader unifying framework that holds a central role for intersexual conflicts over  
339 reproductive control. By integrating concepts from theories of sexual conflict, sexual  
340 selection and social evolution, this new framework generates testable predictions regarding  
341 the ecological and evolutionary landscape of intersexual power within and across  
342 mammalian societies. The scientific investigation of intersexual power is a burgeoning and  
343 interdisciplinary research topic where much conceptual and empirical work remains to be  
344 done. We hope that this framework will be expanded and stimulate further studies (see  
345 Outstanding Questions), notably to develop standardised and widely applicable methods  
346 and transdisciplinary tools to quantify intersexual power in reproductive and social contexts.  
347 We also hope this work will encourage future studies to investigate how resource-holding  
348 power and decisional power (leadership) may interact and influence one another and  
349 ultimately develop a unifying framework for the study of intersexual power across domains,  
350 and across mammalian societies, including humans.

351

352



## Glossary

**Attribute:** 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 others (e.g., social rank, kinship, coalitionary partners).

**Coercion:** 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:** mating system where males aggressively defend reproductive access to multiple females.

**Deception:** 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:** degree of control over resources and reproduction that members of one sex exert over members of the other sex. It shapes – and can thus be measured by – whether and how access to resources and reproduction is gained or retained by individuals of one sex.

**Leverage:** 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:** 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.

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

378 **Motivation:** incentive to engage in potentially costly behaviours or suboptimal trade to gain  
379 or retain access to a resource that is shaped by the value attributed to the resource, as  
380 determined by the individual state or life history.

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

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

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

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

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

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

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

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

399

400 **Figure 1. Relationship between mating system, reproductive control and intersexual**  
401 **power. (A)** A selection of male and female traits proposed as criteria to quantify male-  
402 female biases in reproductive and social control in social mammals as illustrated by nine  
403 exemplary species. Colour tones indicate whether the trait promotes or reflects male control  
404 (blue), female control (red) or neither (yellow); “?” indicates either missing or non-  
405 consensual data in the current literature. Colour darkness reflects the strength of trait  
406 expression and, for overall scores of reproductive control and social control, the  
407 corresponding degree of intersexual bias. Scores of social control were derived from  
408 published indices of social dominance as quantified by the proportions of dyadic agonistic  
409 interactions won by males vs. females. **(B)** Putative position of the nine exemplary species  
410 (black icons) and their mating systems in relation to intersexual power measured along two  
411 axes – reproductive control and social control – as assessed by overall scores in panel A.  
412 Coloured areas delineate the proposed range of association between reproductive and social  
413 control for four mating systems; the gradient of contest- vs. scramble- based competition is  
414 depicted by a double arrow. Intersexual power follows a diagonal from species where power  
415 is strongly male-biased in both contexts (see Hamadryas baboons, *Papio hamadryas*) to  
416 strongly female-biased in both contexts (see ring-tailed lemurs, *Lemur catta*); mammalian  
417 societies where reproductive control is strongly female-biased and social control is strongly  
418 male-biased, or *vice versa*, are unlikely to emerge. Reference list: Hamadryas baboon  
419 [29,46]; chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*, see Box 3); Guinea baboon  
420 (*Papio papio*) [77] ; meerkat (*Suricata suricatta*) [30,78], moustached tamarin (*Saguinus*  
421 *mystax*) [79–83]; rock hyrax (*Procavia capensis*) [17,84]; spotted hyena (*Crocuta crocuta*)  
422 [16,28,85]; ring-tailed lemur [15,49]; cross-specific data [27,36,86].

423

424 **Figure 2. Eco-evolutionary pathways to male and female empowerment in mammals.**

425 Proposed framework to predict intersexual power asymmetries across mammalian societies.

426 There is interplay and feedback between the mating system and asymmetries in

427 reproductive and social control, and outlines the distinct pathways to male- and female-

428 biased power. Coercion and male-biased dimorphism constitute a co-evolutionary highway

429 to male power in species with contest-based polygyny and polygynandry (left side); Female

430 empowerment emerges through diverse physiological, morphological, behavioural, and

431 socio-ecological pathways (right side) in species with scramble-based polygynandrous,

432 monogamous or polyandrous mating systems.

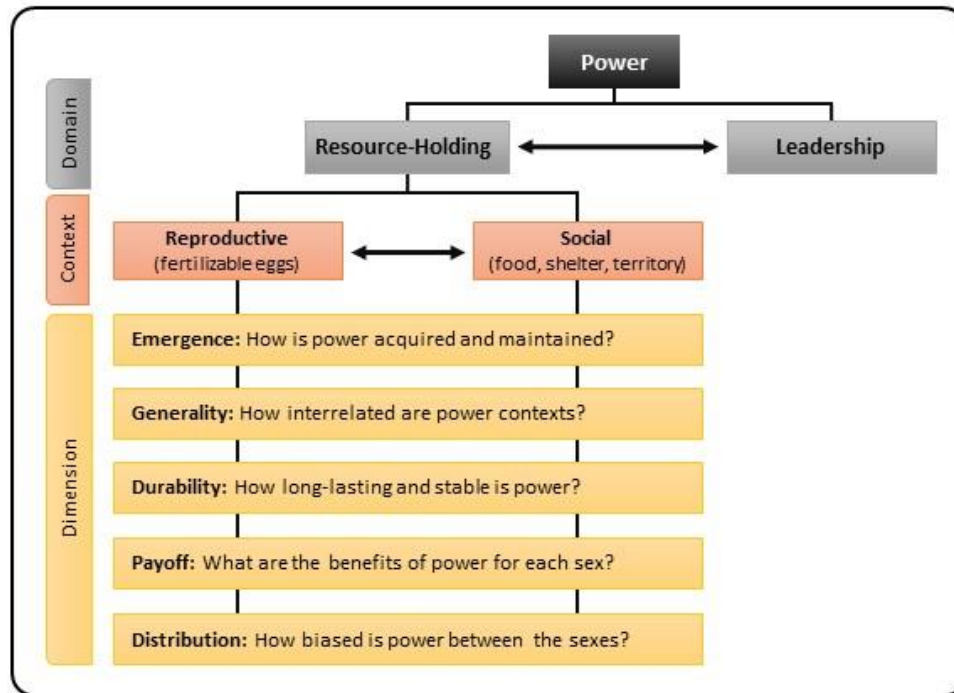
433 **Box 1. The duality of intersexual power: reproductive and social control.**

434 Power can be divided into two main domains, namely resource-holding power and decisional  
435 power (or ‘leadership’) [6,7]. We propose that resource-holding power arises in two main  
436 contexts – namely, reproductive and social contexts – defined according to the nature of the  
437 resource the two sexes compete over [8] (Figure I). Spotted hyenas (*Crocuta crocuta*) nicely  
438 illustrate the duality and context-dependence of intersexual power. In this species, females  
439 have complete reproductive control owing to the peculiar anatomy of their external  
440 genitalia. Females lack a vaginal opening (because their labia are fused) and instead possess  
441 an elongated and erectile clitoris through which they copulate, urinate and give birth [16]. A  
442 direct consequence is that copulation requires the full cooperation of the female and that  
443 females can actively choose when and with whom they mate [85]. In contrast, social control  
444 emerges from asymmetries in the number of recruitable social allies. The extent of  
445 intersexual biases in social control may fluctuate between strictly female-biased power  
446 structures and balanced social power between males and females, depending on the kin and  
447 demographic structure of the groups [28]. Building on previous conceptual categorisation of  
448 dominance [8], power [87] and leadership [11], we further propose that resource-holding  
449 power can be described following five dimensions: distribution (extent of asymmetries  
450 between the sexes), emergence (whether acquired *via* coercion, deception or trade),  
451 durability (stability versus lability), payoffs (sex differences in the fitness benefits to win  
452 intersexual contests) and generality (context-dependence or consistency across contexts)  
453 (Figure I).

454

455 **Figure I. Domains, contexts and dimensions of intersexual power.** The proposed framework  
456 captures the multifaceted nature and variability of intersexual power in animal societies. Bi-

457 directional arrows indicate the inter-dependence and potential feedback among domains  
 458 and contexts of power. We here focus on the categorisation of power that emerges from the  
 459 resource-holding domain.



460

461

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

464 Asymmetries in reproductive control between males and females may vary in predictable  
 465 ways across mating systems. We illustrate such covariation along a gradient across the six  
 466 baboon species, before generalising (Figure 1). At one end, Hamadryas baboons (*Papio*  
 467 *hamadryas*) exhibit contest-based **polygyny** with full male reproductive control; males are  
 468 much larger than females and maintain exclusive access to multiple females by forcibly  
 469 herding females away from their natal group, thereby breaking-up their social ties and  
 470 support. Leaders of such one-male units use various coercive strategies including infanticide

471 after take-overs, and neck-biting when females leave their vicinity [29]. Next, chacma baboons  
472 (*P. ursinus*) exhibit predominantly **contest-based polygynandry**. They live in large multimale-  
473 multifemale groups with high male reproductive skew – i.e., where access to mates is  
474 monopolised by a few males – and intense sexual coercion, including mate-guarding,  
475 intimidation and infanticide [88]. Unlike Hamadryas females, chacma females mate  
476 promiscuously before ovulation and remain in their natal group; they can form alliances with  
477 kin and adult males to seek protection against other coercive males [54]. Next are yellow (*P.*  
478 *cynocephalus*), olive (*P. anubis*) and then Guinea baboons (*P. papio*), with a progressive  
479 decline in male reproductive skew, sexual dimorphism and coercion, and a concomitant  
480 increase in the degree of female reproductive control. Females of these species may shorten  
481 or evade mate-guarding bouts by using fertility signals to exacerbate costly male-male  
482 competition [44], by resisting mate-guarding attempts or by mating sneakily with other males  
483 [89]. In Guinea baboons, males maintain long-term social and sexual bonds with maximum  
484 two females, females can freely disperse to other social units and infanticide is unreported  
485 [77]. Finally, in Kinda baboons (*P. kindae*), females mate promiscuously even in the ovulatory  
486 period, male reproductive skew is low and there is no evidence of infanticide [90]. Unlike other  
487 species, Kinda baboons breed seasonally and live in very large groups (>200 individuals). These  
488 features likely restrict male reproductive control and triggered an evolutionary shift from  
489 contest-based to **scramble-based** polygynandry – where male-male competition primarily  
490 occurs *via* sperm competition – as suggested by their low sexual dimorphism, relatively large  
491 testes and the fact that males queue rather than fight over rank [90]. This gradient illustrates  
492 general links between the mating system, reproductive control and intersexual power (Figure  
493 1): as female reproductive control grows, contest-based mating systems are progressively  
494 replaced by scramble-based systems, associated with more balanced intersexual power.

495 These changes in reproductive control likely emerge from the combined effect of passive  
496 ecological and demographic processes (e.g., increased group size) and of strategies used by  
497 females to resist male monopolization attempts. Where males retain partial reproductive  
498 control, but where reproductive competition between females is too high to allow group-  
499 living, **monogamy** may initially evolve as a form of permanent mate-guarding [91], decreasing  
500 subsequent sexual conflict and paving the way to more equal reproductive control between  
501 the sexes and less-coercive mechanisms of intersexual power.

502

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

504 Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) live in multimale-multifemale  
505 groups in equatorial Africa. In both species, males typically remain in their natal group and  
506 females disperse [92]. Their common ancestor likely exhibited male-biased power, as all Great  
507 Apes except bonobos [92].

508 In chimpanzees, adult males dominate adult females and have priority over access to high-  
509 value resources like meat [92]. In bonobos, females win most dyadic conflicts against males  
510 and enjoy privileged access to meat [23,92,93]. Females in both species exhibit genital  
511 swellings when sexually receptive, but bonobo females exhibit more and longer swollen  
512 periods during an interbirth interval [45]. Consequently, the swellings of female bonobos  
513 advertise fertility less reliably than those of female chimpanzees [45,94]. Chimpanzee males  
514 can commit infanticide, are frequently coercive towards receptive females [95], and alpha  
515 males have the highest reproductive success, because they can effectively mate-guard  
516 females throughout their ovulatory period [94,96]. In contrast, bonobo males are not  
517 infanticidal nor sexually coercive, they fight less over females, and the high male reproductive  
518 skew likely reflects differences in maternal support [97,98].



519 Following our framework, the initial step towards loss of male-biased power may be the  
520 confusion of ovulation, preventing male bonobos from monopolising receptive females and  
521 concurrently increasing female reproductive control. This probably reduced the payoff and  
522 incentive of males to fight over females, leading to a shift towards scramble-based  
523 polygynandry (Figure 1) – as suggested by the relatively larger testes and decreased sexual  
524 dimorphism in bonobos compared to chimpanzees [92]. Increased female promiscuity likely  
525 further led to the disappearance of male infanticide and sexual coercion. In line with this, male  
526 chimpanzees seem more coercive in populations where female fertility signals are shortest  
527 (presumably most reliable) [99]. Female-biased control over resources probably evolved  
528 secondarily in relation to their ability to use leverage and exercise mate choice [23,24]. In  
529 contrast to males, female bonobos maintain strong relationships, which may be favoured by  
530 prolonged sexual receptivity [100,101]; they can form coalitions against males and interfere  
531 in male-male competition to support their sons [92,93,97]. Such male-female differences in  
532 cooperation likely reinforced female reproductive and social control [92,93,100] rather than  
533 constituted the initial step towards female empowerment. Overall, current evidence is  
534 compatible with the scenario that strong contrasts in mating system, intersexual power and  
535 social behaviour in chimpanzees and bonobos emerged from subtle changes in female  
536 reproductive control.

537

538

### 539 **Acknowledgements**

540 We thank O.P. Höner for his contribution on early versions of the manuscript and figures; M.

541 Cant and two anonymous reviewers for insightful comments on the manuscript. Silhouette

542 icons of chimpanzee, bonobo and Guinea baboon in figure 1 were downloaded from

543 <http://phylopic.org> (credit to T. Michael Keeseey and Owen Jones); all other animal icons  
544 were drawn by E. Davidian. E.D. received financial support from the Sopa Society.

545

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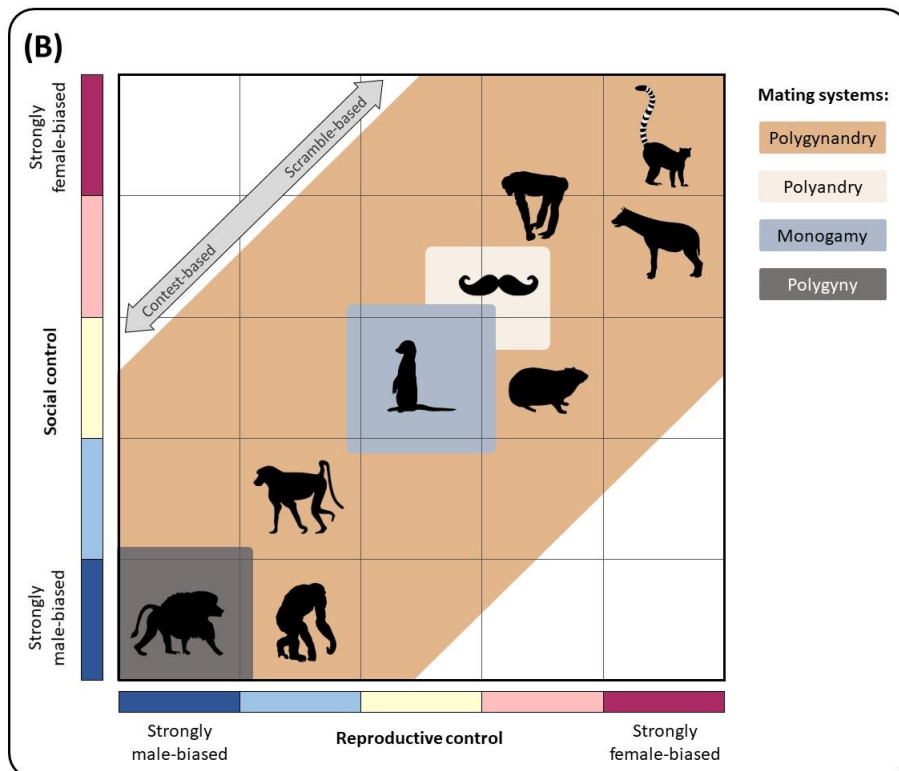
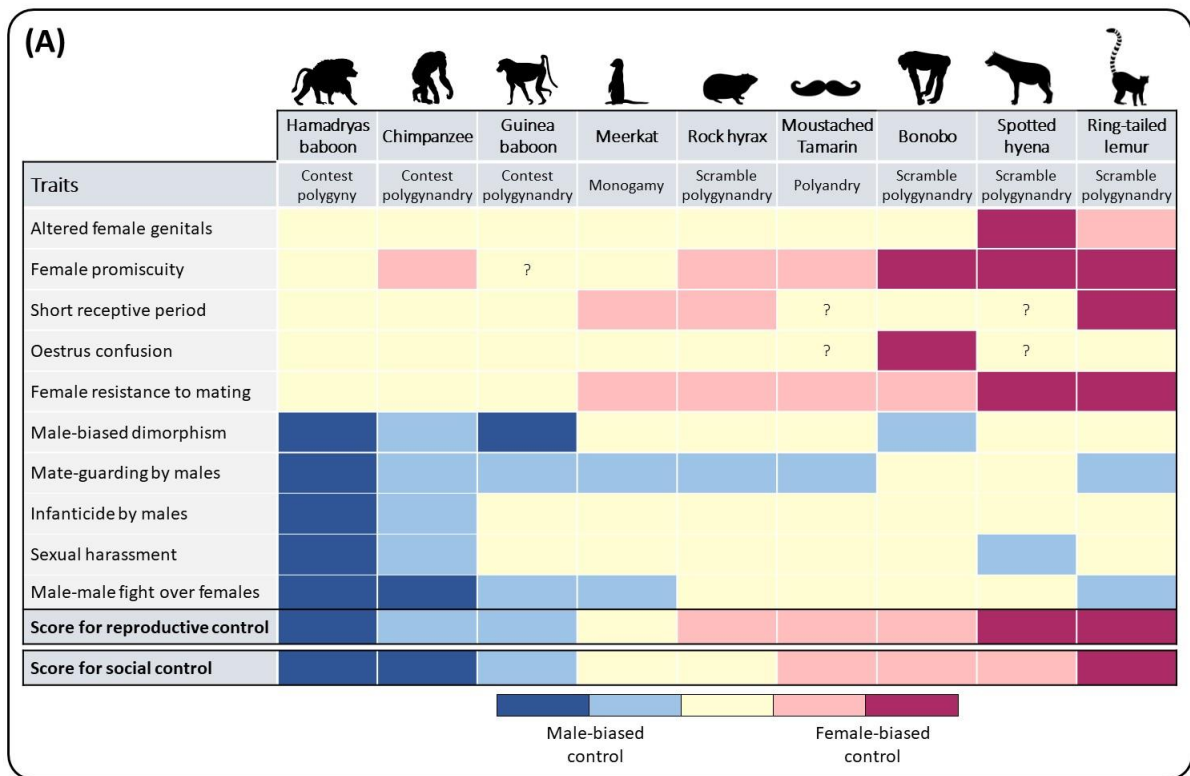
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762 Figure 1



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