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Socially bonded females face more sexual coercion in a female-philopatric primate

Female-male bonds increase the risk of sexual coercion

Stronger bond with a certain male

More coercion from him

More coercion from all other males

More socially integrated females face more sexual coercion from all males

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Highlights

Female mandrills faced the most sexual coercion from their top male partners

Females that are overall more bonded with adult males faced more sexual coercion

Females more integrated in the female social network faced more sexual coercion

Overall, this study shows that social bonds can be a risk factor for sexual coercion
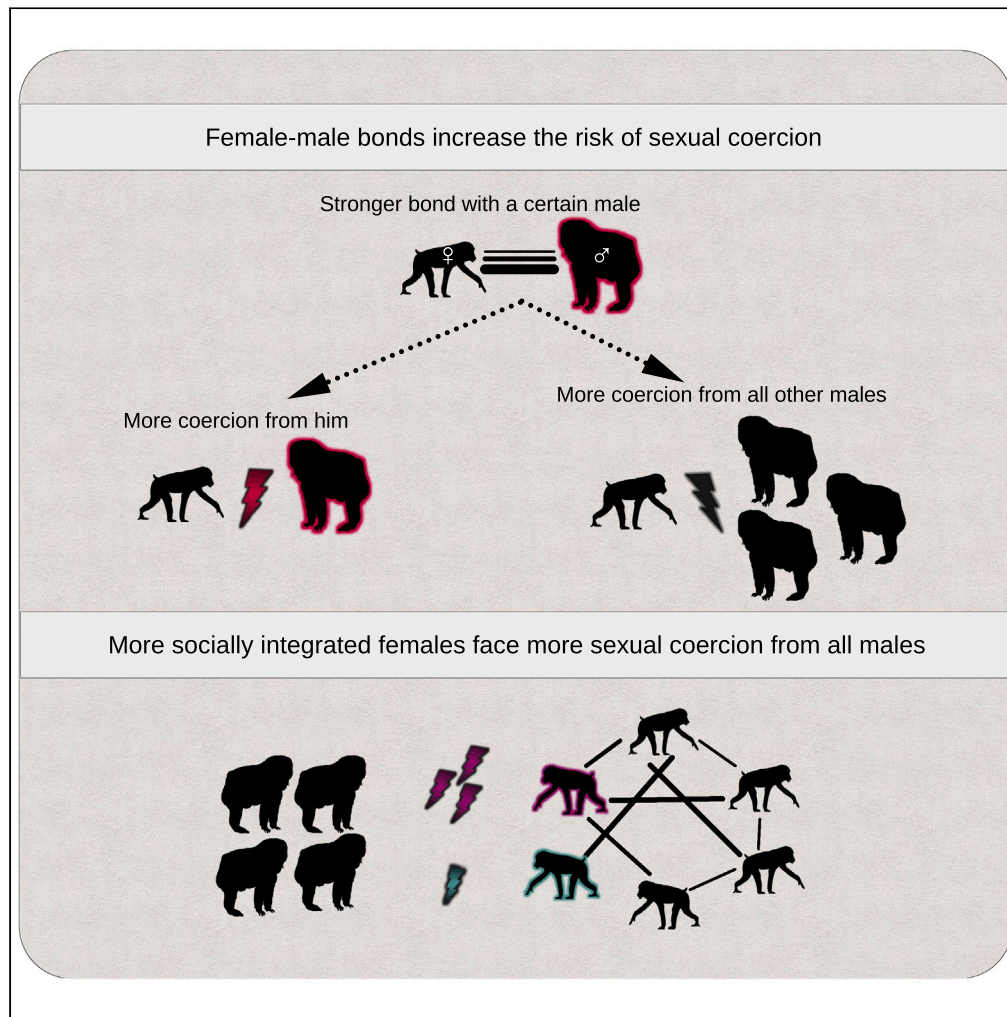
Article

Socially bonded females face more sexual coercion in a female-philopatric primate

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SUMMARY

Sexual coercion is a manifestation of sexual conflict increasing male mating success while inflicting costs to females. Although previous work has examined inter-individual variation in male sexually coercive tactics, little is known about female counter-strategies. We investigated whether social bonding mitigates the extent of sexual coercion faced by female mandrills (*Mandrillus sphinx*), as a putative mechanism linking sociality to fitness. Surprisingly, females faced the most coercion from those males with whom they formed the strongest bonds, while the strength of a female-male bond was also positively correlated with coercion from all other males. Finally, greater social integration in the female network was positively correlated with coercion, through a direct 'public exposure' mechanism and not mediated by female reproductive success or retaliation potential. Altogether, this study shows that neither between- nor within-sex bonds are protective against sexual coercion and identifies, instead, a hidden cost of social bonding.

INTRODUCTION

The attempt to control reproductive opportunities is a fundamental aspect of animal social evolution[1] that often leads to within-sex competition[2] and between-sex conflict.[3] Sexual conflict emerges from the diverging evolutionary interests of males and females and appears ubiquitous from insects to mammals.[4] Sexual coercion, often described as a third form of sexual selection,[5,6] is one behavioral manifestation of sexual conflict, in which males use aggression (often inflicting injuries[7] or stress[8]) toward females to increase their mating success.[5,9] A few recent studies have investigated the benefits of coercion to males,[10] or the sources of variation among males in coercive tendencies.[11] Much less is known, however, about the strategies used by females to mitigate their exposure to coercion and its associated costs.

In response to sexual conflict, females may develop physiological adaptations to minimize male monopolization potential, such as synchronizing sexual receptivity[12] to dilute male coercion or manipulating the detectability[13,14] or reliability[15] of fertility signals to deceive males.[16] They may also use behavioral strategies, such as sneaky copulations,[17] promiscuous mating[18] or some form of social defense.[19,20] Females might, specifically, use alliances with males or other females to prevent or resist male coercive tactics.[5] To date, the only relevant studies have focused on the protective effect of female-male bonds against infanticide across several species[21] or against sexual harassment in orangutans.[19] Therefore, female social relationships with males or other females might mitigate sexual coercion in ways that have not been investigated yet.

A large body of work highlights the positive effect of social relationships on fitness across many taxa, but the mechanisms mediating these effects remain partially understood.[22] Social relationships may protect against chronic social stress[23,24] and conspecific harassment.[25] Between-sex bonds, in particular, are associated with a reduced risk of social harassment and mortality in female baboons and humans.[26–30] Thus, females may form long-term associations with certain males to minimize the risk of conspecific aggression.[31] In addition, females may sustain stronger bonds with certain males to reduce aggression from them,[32] possibly because affiliation allows males to mate with their female associates without using coercion. Lastly, female-female bonds might also prove protective. In South American sea lions (*Otaria flavescens*), females breed in large groups to dilute the risk of male harassment[33] and in feral horses, more socially integrated females face less male social harassment[34] perhaps because males are reluctant to assault bonded females who could form coalitions to retaliate against them.[5,35] Notably, female-female coalitions have likely contributed to prevent the evolution of sexual coercion in bonobos[36] in contrast to the congeneric sexually coercive chimpanzees[8] where such coalitions are rare.[37] Overall, the fitness benefits of social bonds may be partially mediated by their protective effect against aggression, including sexual coercion, but this 'protective bonds' hypothesis has received limited attention in the sexual selection framework.

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Social bonds might, contrarily, be associated also with costs in the context of sexual coercion ('costly bonds' hypothesis). First, strongly socially connected females often enjoy higher reproductive success than poorly connected ones,[34,38] potentially attracting male mating interest and coercion. For example, male chimpanzees (*Pan troglodytes*) prefer mating with older, parous females because they show higher reproductive success than younger ones,[39] likely explaining why parous females also face more coercion.[8] Second, affiliation history often predicts coalition formation in mammals.[40,41] Highly socially connected females might thus enjoy greater coalitionary support that they could use to retaliate more frequently in response to coercive males (similarly to powerful women who respond assertively against their coercers[42,43]), which in turn might increase the risk of escalation by males. Finally, females who occupy central positions in a group's social network typically interact more with their groupmates, potentially leading to higher spatial 'centrality', exposing them to greater coercion simply because they are more visible and encounter males more often than peripheral females.

Here, we test the influence of female-male social bonds and female-female social integration on the intensity of male sexual coercion that females face, using a 9-year dataset on wild mandrills. Mandrills are seasonally breeding primates of the *Cercopithecidae* family, living in large polygynandrous groups.[44] Males are 3.5-times heavier than females[45] and this physical asymmetry probably facilitates males to obtain mating opportunities through sexually coercive strategies rather than bribing females by offering services. Indeed, males rarely groom females but they often mate-guard those who display large sexual swellings around ovulation.[46] Additionally, a recent study has shown that male aggression before the swelling phase of a female's estrus cycle increases male mating success during the subsequent swelling phase.[47] Thus, male aggression occurring before the swelling phase qualifies as sexual coercion (i.e., sexual intimidation), while aggression occurring during the swelling phase does not, since it is not associated with male mating success.[47] Nonetheless, male mandrills may also potentially protect females: they are occasionally observed directing aggression to rivals who previously directed aggression to females and they might also enter coalitions of females that chase rival males away, regardless of the dominance rank asymmetry among males (NS personal observation). While most males enter the group at the onset of the mating season and often leave afterward, females are philopatric[48] and therefore, they might depend more on their more stable bonds with other females in order to defend themselves against males. Indeed, female-female bonds appear to be crucial in this species: social integration (measured as the number of individuals a female affiliates with or her rate of overall affiliation) is positively correlated with both dominance rank[49] and younger age at first reproduction.[38] Females can thus form strong social bonds with kin[50,51] that occasionally translate into coalitions against other groupmates. Notably, coalitions of females can chase away or sometimes even physically attack males.[52]

We made the following predictions with respect to the protective bonds' hypothesis in a mating context: (P1) female mandrills who form strong bonds with males face less coercion from them; (P2) females who form strong bonds with their 'top male partners' face less coercion from all other males; and (P3) females who are well-connected in the female social network and/or have larger matrilines face less male coercion overall. Because our results were opposite to those predicted, supporting rather the costly bonds' hypothesis, we further tested whether well-connected females face more coercion because they (1) have higher reproductive success and thus are more attractive to males ('reproductive success' indirect path), (2) are high-ranking and are thus likely to retaliate against coercive males ('retaliation' indirect path), or (3) occupy central positions in the social network, which may expose them to more coercion ('public exposure' direct path).

RESULTS

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

Female-male dyads who exchanged more grooming were also characterized by higher coercion rates (Figure 1A; Table 1). Similarly, in dyads with higher proximity scores, males were more coercive (Chisq = 26.190, p value < 0.001; Figure 1B). Particularly, one standard deviation increase in grooming or proximity score was associated with 0.25 and 0.42 additional aggression events, respectively. Males in their prime were more coercive than younger and older ones (Table 1). Moreover, there was a marginally non-significant trend for older females to face more coercion (Table 1). All other variables, including male-female rank difference, were not significant (Table 1). Results were qualitatively similar when adding male and female rank as two explanatory variables instead of male-female rank difference (not shown).

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

The bond of a female with her top male partner did not protect her against coercion from other males. Instead, females who exchanged more grooming with their top grooming partner received more coercion from all other males (Figure 1C; Table 2). Particularly, one standard deviation increase in grooming rate was associated with 0.49 additional aggression events. However, females who stood closer to their top proximity partner did not face more or less coercion from other males (Chisq = 2.231, p value = 0.135). All other variables did not influence the results.

Does female integration in the female-only network or the number of maternal kin in the group protect her against male coercion (P3)?

We found that more central females (i.e., with higher eigenvector centrality; Figure 2A; Table 3) and those with higher strength (Chisq = 9.490, p value = 0.002; Figure 2B) in the female-only grooming network faced more sexual coercion from all males. Additionally, females with larger matrilines also faced more coercion (Chisq = 4.288, p value = 0.038; Figure 2C) though the corresponding model did not control for female rank which was correlated with matriline size (when adding female rank, the effect of matriline size became marginally non-significant Chisq = 3.00, p value = 0.08). Finally, there was a marginally non-significant trend for higher-ranking females to face more coercion (Table 3). Female age and the operational sex ratio did not influence the results.
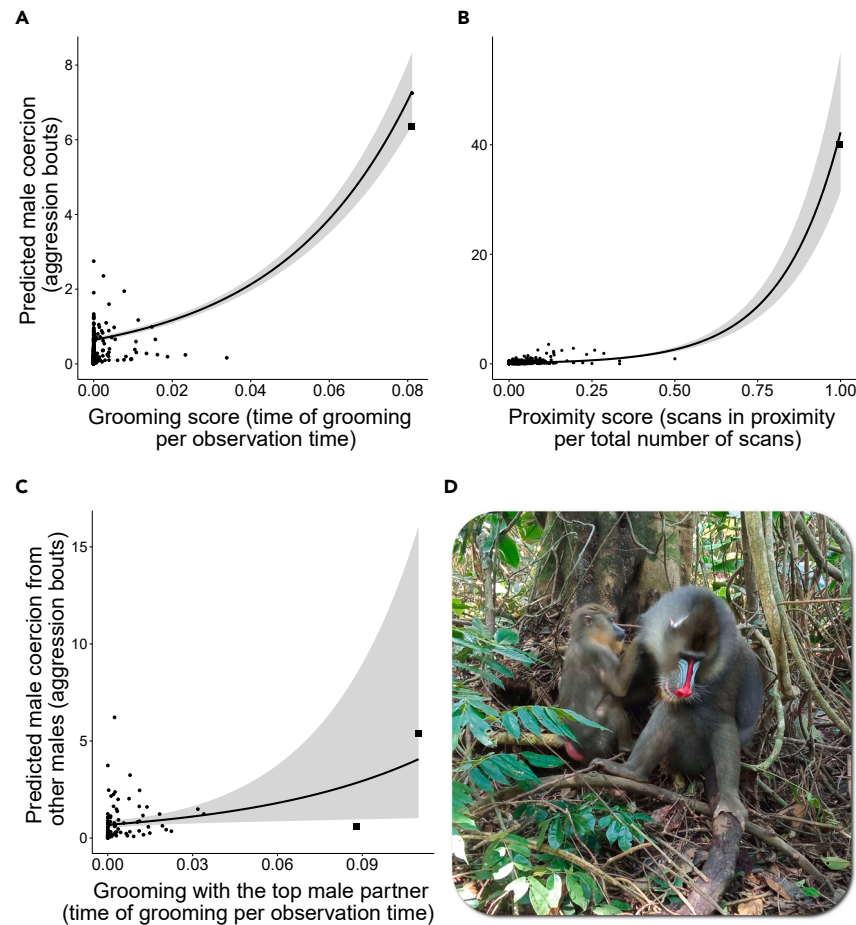
Figure 1. Coercion faced by females as a function of female-male dyadic affiliation rates

(A and B) Coercion within a dyad as a function of the rate of (A) grooming and (B) proximity of the dyad.

(C) Coercion faced by a female from all males except her top grooming partner as a function of the strength of her grooming rate with him. Grooming rates correspond to the time spent by the female grooming the male divided by the total time of observation of each dyad. Proximity rates correspond to the number of scans for which the dyad was recorded in proximity divided by the total number of scans of the dyad. The regression lines of the GLMMs are shown. Shaded areas show 95% confidence intervals. The results hold with or without including the outliers (squares).

(D) An adult, cycling female mandrill grooming an adult male.

Is the effect of female centrality on sexual coercion direct, or indirectly mediated by female reproductive success or retaliation potential?

The mediation (path) analysis suggested that the correlation between female centrality in the female-only grooming network and sexual coercion was independent from our proxies of female reproductive success and female retaliation potential, failing to support the 'reproductive success' and 'retaliation' indirect paths (Figure 2D Table 4). In contrast, female centrality positively and directly correlated with the coercion a female faced, supporting the 'public exposure' direct path (Figure 2D; Table 4). This effect did not appear to be a simple byproduct of female-male association because the model considering a female's overall spatial proximity to males on the probability of coercion from all males performed worse than the model including female centrality (Δ AIC = 42.47); and the overall spatial proximity to males was marginally non-significant (Chisq = 3.60, p value = 0.058). Finally, female rank and age were positively correlated with reproductive success but they did not influence the probability of facing sexual coercion (Table 4).

DISCUSSION

Social bonds and social integration are associated with important fitness benefits in several species (longevity[22]; reproductive success[34]) including mandrills.[38] We therefore investigated whether they also mitigate the intensity of sexual coercion that females face, providing a putative behavioral mechanism mediating the link between sociality and fitness. Our results highlight that social bonding is, indeed, a crucial factor modulating the expression of sexual coercion[53] but not in the direction proposed by our central hypothesis. Specifically, we found that

Table 1. Drivers of variation in the intensity of sexual coercion within female-male dyads

Response variable: Aggression from the dyad male

Fixed factor	Estimate	CI 95%	Chisq	P-value
Grooming score	53.939	[14.580;93.298]	7.215	**0.007**
Rank difference	−0.188	[-5.222; 4.846]	0.005	0.942
Operational sex ratio	1.635	[-0.691; 3.961]	1.899	0.168
Female age	0.061	[-0.011; 0.133]	2.773	0.096
Male age	−3.617	[-12.178; 4.944]	7.695	0.408
Male age^2	−14.032	[-23.982;-4.081]	7.695	**0.006**

The analysis included 801 intersexual dyads (composed of 51 females and 39 males). Significant p values and confidence intervals that did not cross zero appear in bold. The significance of each variable was assessed using chi-square tests (Chisq).

social bonding failed to confer any protection against sexual coercion in mandrills. Instead, females with stronger bonds with either males or females faced more coercion, revealing a hidden cost of sociality ('costly bonds' hypothesis).

Female mandrills received more coercion from males with whom they formed stronger bonds. In hamadryas baboons (*Papio hamadryas hamadryas*) and bottlenose dolphins (*Tursiops aduncus*), males aggressively enforce proximity with females to reduce the chances that they will mate with rival males.[54,55] Mandrill females might accordingly be forced into spatial associations maintained by coercive males, similar to mate-guarding episodes, which can simply reflect male mating strategies rather than female initiated affiliation. However, unlike hamadryas baboons or bottlenose dolphins, male mandrills rarely, if ever, use overt physical restraint, sequestering or 'herding' behaviors toward females; but they rather coerce females using milder aggressive tactics.[47] While directional grooming of females toward males may be less easily enforced by males than spatial proximity, a recent study in sexually coercive chacma baboons (*Papio ursinus*)[7] indicates that females may regularly groom males as an appeasement strategy.[56] In mandrills, females have been occasionally observed to groom males after receiving aggression from them (NS personal observation), suggesting that a similar appeasement strategy might explain our results.

It is also possible that the higher rate of coercion within bonded dyads is a simple by-product of dyad members' spatial proximity, because greater proximity may create more opportunities for coercion. Nevertheless, at least two points speak against this interpretation. First, while affiliation and coercion can co-exist within female-male bonds, female-male bonds do not necessarily entail any violence even in species in which males use sexual coercion. For example, in chacma baboons, the social bonds formed between a male and a lactating female around an infant are typically characterized by high spatial proximity and frequent grooming but very low levels of male aggression toward the female.[57,58] Second, we found that overall proximity to males is not strongly correlated with the probability of facing coercion from all males in mandrills, suggesting that proximity alone cannot account for most variation in the intensity of coercion.

Male mandrills also did not provide protection to their female partners against sexual coercion from other males. While a male mandrill might repel rivals during short mate-guarding bouts in the few days around ovulation in the mating season, he might not gain any additional benefits from protecting a female outside these bouts. Finally, given that the highest-ranking males are also the most coercive in mandrills,[47] a male would likely face high risks–regardless of his own rank–when confronting these high-ranking coercers to protect his female partner. Instead of a protective effect, we unexpectedly found that female mandrills sharing stronger bonds with their top grooming partner received more coercion from other males, but the reasons for that are not yet clear. In fact, this result might reflect a male competitive strategy, where males harass and intimidate their rivals' mates to disrupt their social bonds[59] or provoke confrontations that they are likely to win.[60] Alternatively, it may be caused by an unidentified confounding factor, such as a higher sexual attractiveness of such females, who would make them preferential targets of coercion.

Table 2. Female grooming bonds with their top male grooming partner in relation to sexual coercion from all other males (n = 97 estrus cycles of 46 females)

Response variable: Aggression from all males except the male partner

Fixed factor	Estimate	CI 95%	Chisq	P-value
Grooming strength	31.530	[16.036;47.025]	15.907	**< 0.001**
Female rank	−2.250	[-10.568; 6.069]	0.281	0.596
Partner rank	−11.216	[-36.814; 14.382]	0.737	0.390
Female age	0.045	[-0.082; 0.172]	0.479	0.489
Operational sex ratio	3.406	[-0.762; 7.575]	2.565	0.109

Significant p values and confidence intervals that did not cross zero appear in bold. The significance of each variable was assessed using chi-square tests (Chisq).
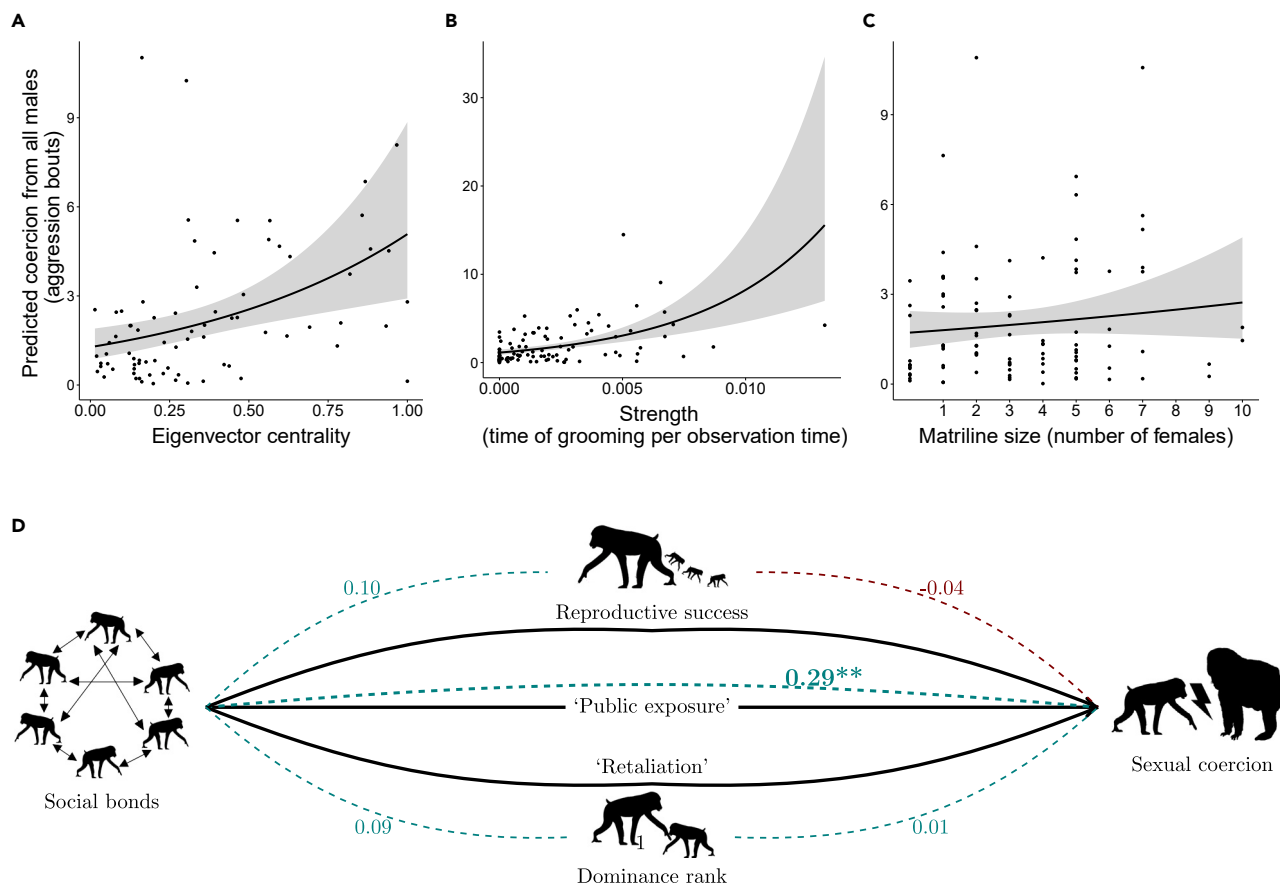
Figure 2. Coercion faced by females as a function of their integration in the female social network

(A–D) Predicted coercion faced from all males as a function of a females' (A) eigenvector centrality and (B) strength in the female grooming network, as well as of (C) her matriline size. The regression lines of the GLMMs are shown. Shaded areas show 95% confidence intervals. Panel (D) illustrates the path analysis, including the hypothetical direct and indirect effects of female social bonds on coercion faced from all males (solid black lines). The different effects may follow two indirect paths, respectively mediated by female reproductive success ('reproductive success'; top solid line) and dominance rank ('retaliation'; bottom solid line), as well as a direct path ('public exposure'; middle solid line). Dashed line color represents positive (teal) or negative (red) relationships, along with the estimates. Only the direct path, 'public exposure', was significant (in bold).

Earlier hypotheses propose that female aggregations and alliances may represent counterstrategies to sexual coercion.[5,36,61] In contrast, we found that more socially integrated female mandrills (with higher centrality or strength in grooming networks or larger matrilines) face more sexual coercion, despite their occasional violent coalitions against males.[52] The results of our path analysis did not support the 'reproductive success' indirect path proposing that male coercion preferentially targets central females because these have higher reproductive success – and might be thus more attractive to males. Nevertheless, other proxies of female attractiveness might be more suitable than reproductive success. Male mating effort typically varies with female fertility, which can be advertised by sexual swelling size in cercopithecids.[62] A future study using a combination of swelling size and hormonal measures of fertility might help to clarify the association between female attractiveness and male coercion. Similarly, the results of our path analysis did not support the 'retaliation' indirect path: female centrality did not predict rank and rank did not mediate the effect of centrality on coercion. Finally, in contrast to previous results[47] (see also Table 3) our path analysis suggested that female rank is not associated with coercion (Table 4), calling for future studies using, for example, more fine-grained estimations of female rank, to clarify this association, or lack thereof.

More socially integrated females in the female-only network appeared to face more sexual coercion ('public exposure' direct path), likely because they are more central in the social life of the group and are thus more visible or spatially close to coercive males. Such interpretation may explain why females who are more socially connected with both males and females face more coercion. Social and spatial centrality are associated with lower predation risk[63] and male primates are commonly the main defenders of social groups against predators.[64] Our results highlight that female primates who live in groups with males might experience trade-offs between these predation related benefits and sexual coercion. Moreover, although the risk of sexual or social coercion are often higher for socially isolated females in some species (humans[65]; feral horses[34]), our results echo observations in white-faced capuchins (*Cebus capucinus imitator*) where new alpha males preferentially kill infants of strongly socially connected and central females,[66] indicating that social connections may represent a risk factor for sexual coercion

Table 3. Female-female social bonds and sexual coercion (n = 77 estrus cycles of 39 females)

Response variable: Aggression from all males

Fixed factor	Estimate	CI 95%	Chisq	P-value
Female centrality	0.939	**[0.147;1.732]**	5.399	**0.020**
Female rank	0.720	[-0.032; 1.473]	3.517	0.061
Female age	−0.046	[-0.109; 0.016]	2.140	0.143
Operational sex ratio	0.671	[-1.964; 3.306]	0.249	0.618

Significant p values and confidence intervals that did not cross zero appear in bold. The significance of each variable was assessed using chi-square tests (Chisq).

in some societies. Finally, our results might reflect alternative pathways that we could not test for. For example, recent studies suggest that social bonds and support can influence woman health and fertility.[67,68] Thus, male primates might prefer to mate with (and coerce the most) central females because of their better health or higher fertility.

These results add to a growing literature describing the costs of social integration and social bonds. For example, social integration is associated with reduced offspring survival in female eastern gray kangaroos (*Macropus giganteus*;[69]) and reduced longevity in yellow-bellied marmots (*Marmota flaviventer*).[70] Nonetheless, these currently appear as exceptions in a broader picture in which social integration is beneficial for individual fitness.[22] Placing our findings into this picture requires comparing the possible costs of coercion with the overall benefits of social integration on female reproductive success and survival. Although sexual coercion is associated with an increased risk of injury for female mandrills,[47] these costs might be short-lived, i.e., concentrated during a relatively short period before conception. Conversely, the benefits of social bonding might be long-lasting and independent of life stage or reproductive state. Ultimately, although our study might reveal a potential mechanism through which sexual conflict shapes social evolution, further studies need to clarify the strength of its selective pressure.

Previous hypotheses suggest that female social alliances represent a primary line of defense against male sexual coercion. We expected this to be particularly overt in mandrills where female alliances are regularly observed and the extreme male-biased sexual size dimorphism likely prevents unaided female defense against males. Conversely, our results showed that neither female alliances nor female-male bonds confer such defense. Thus, our results call for the extension of a burgeoning field that investigates the social ecology of sexual coercion in other societies, focusing, in particular, on the effect of social environment on the use and forms of male coercive strategies, as well as the risks and costs of coercion faced by females.

Limitations of the study

Our study suffers from some limitations. First, it is observational, and thus does not allow us to make any firm inference on the causal relationships linking female social bonds and male sexual coercion, which could be generated by confounding factors. In addition, the large size of our study group as well as the dense vegetation and low visibility limited the resolution of our behavioral data for some individuals or heterosexual dyads. Finally, our results were opposite to our predictions and revealed an unexpected positive correlation between the variables of interest, making the interpretation more complex and fragile. Nonetheless, the relationship linking social bonds and coercion was consistently positive across different types of social partners and connections (i.e., the strength of male-female dyadic bonds, the strength and number of female-female bonds), and we propose several interpretative scenarios for it.

Table 4. Direct and indirect effects of female-female social bonds on sexual coercion

Paths to coercion

Term	Predictor	Estimate(unstandardized)	SE	P
Female rank	Centrality	0.098	0.118	0.405
	OSR	0.049	0.179	0.785
	Female age	−0.014	0.008	0.082
Rep. Success	Centrality	0.893	0.647	0.168
	Female rank	2.546	0.633	**< 0.001**
	Female age	0.425	0.044	**< 0.001**
Aggression	Rep. Success	−0.005	0.020	0.791
	Female rank	0.013	0.122	0.917
	Centrality	0.298	0.116	**0.010**
	Female age	−0.003	0.011	0.808
	OSR	0.224	0.173	0.197

The path analysis included 77 estrus cycles of 39 females. Significant p values appear in bold.

STAR★METHODS

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AUTHOR CONTRIBUTIONS

Conceptualization, N.S., E.H., and M.J.E.C.; Methodology, N.S., E.H., and M.J.E.C.; Formal Analysis, N.S.; Data collection, N.S., J.D., and L.S.; Data Curation, N.S., M.J.E.C., and J.D.; Writing - Original Draft, N.S.; Writing - Review and Editing, N.S., E.H., and M.J.E.C.; Visualization, N.S.; Supervision, E.H. and M.J.E.C.; Funding Acquisition, M.J.E.C., E.H., and N.S.

DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

1. Clutton-Brock, T. (2021). Social Evolution in Mammals. Science 373, eabc9699. https://doi.org/10.1126/science.abc9699.

2. Clutton-Brock, T., and Huchard, E. (2013). Social Competition and Its Consequences in Female Mammals: Female Reproductive Competition in Mammals. J. Zool. 289, 151–171. https://doi.org/10.1111/jzo.12023.

3. Davidian, E., Surbeck, M., Lukas, D., Kappeler, P.M., and Huchard, E. (2022). The Eco- Evolutionary Landscape of Power Relationships between Males and Females. Trends Ecol. Evol. 37, 706–718. https://doi.org/10.1016/j.tree.2022.04.004.

4. Parker, G.A. (1979). Sexual selection and sexual conflict. In Sexual Selection and Reproductive Competition in Insects, M.S. Blum and N.A. Blum, eds. (Elsevier), pp. 123–166. https://doi.org/10.1016/B978-0-12-108750-0.50010-0.

5. Smuts, B.B., and Smuts, R.W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. In Advances in the Study of Behavior, 22, P.J.B. Slater, M. Milinski, C.T. Snowdon, and J.S. Rosenblatt, eds. (Elsevier), pp. 1–63. https://doi.org/10.1016/S0065-3454(08)60404-0.

6. Clutton-Brock, T.H., and Parker, G.A. (1995). Sexual Coercion in Animal Societies. Anim. Behav. 49, 1345–1365. https://doi.org/10.1006/anbe.1995.0166.

7. Baniel, A., Cowlishaw, G., and Huchard, E. (2017). Male Violence and Sexual Intimidation in a Wild Primate Society. Curr. Biol. 27, 2163–2168.e3. https://doi.org/10.1016/j.cub.2017.06.013.

8. Muller, M.N., Kahlenberg, S.M., Emery Thompson, M., Wrangham, R.W., and Wrangham, R.W. (2007). Male Coercion and the Costs of Promiscuous Mating for Female Chimpanzees. Proc. Biol. Sci. 274, 1009–1014.

1612. https://doi.org/10.1098/rspb. 2006.0206.

9. Muller, M.N., and Wrangham, R.W. (2009). In Sexual Coercion in Primates and Humans: An Evolutionary Perspective on Male Aggression against Females (Harvard University Press).

10. Feldblum, J.T., Wroblewski, E.E., Rudicell, R.S., Hahn, B.H., Paiva, T., Cetinkaya-Rundel, M., Pusey, A.E., Gilby, I.C., and Gilby, I.C. (2014). Sexually Coercive Male Chimpanzees Sire More Offspring. Curr. Biol. 24, 2855–2860. https://doi.org/10.1016/j.cub.2014. 10.039.

11. Reddy, R.B., Langergraber, K.E., Sandel, A.A., Vigilant, L., and Mitani, J.C. (2021). The Development of Affiliative and Coercive Reproductive Tactics in Male Chimpanzees. Proc. Biol. Sci. 288, 20202679. https://doi.org/ 10.1098/rspb.2020.2679.

12. Ostner, J., Nunn, C.L., and Schülke, O. (2008). Female Reproductive Synchrony Predicts Skewed Paternity across Primates. Behav. Ecol. 19, 1150–1158. https://doi.org/10.1093/ beheco/arn093.

13. Schoröder, I. (1993). Concealed Ovulation and Clandestine Copulation: A Female Contribution to Human Evolution. Ethol. Sociobiol. 14, 381–389. https://doi.org/10. 1016/0162-3095(93)90026-E.

14. Heistermann, M., Ziegler, T., van Schaik, C.P., Launhardt, K., Winkler, P., Hodges, J.K., and Hodges, J.K. (2001). Loss of Oestrus, Concealed Ovulation and Paternity Confusion in Free-Ranging Hanuman Langurs. Proc. Biol. Sci. 268, 2445–2451. 1484. https://doi.org/10.1098/rspb.2001.1833.

15. Douglas, P.H., Hohmann, G., Murtagh, R., Thiessen-Bock, R., and Deschner, T. (2016). Mixed Messages:Wild Female Bonobos Show High Variability in the Timing of Ovulation in Relation to Sexual Swelling Patterns. BMC Evol. Biol. 16, 140. https://doi. org/10.1186/s12862-016-0691-3.

16. Palombit, R.A. (2014). Sexual conflict in nonhuman primates. In Advances in the Study of Behavior, 46, M. Naguib, S.D. Healy, J.C. Mitani, L.W. Simmons, H.J. Brockmann, T.J. Roper, and L. Barrett, eds. (Elsevier), pp. 191–280. https://doi.org/10.1016/B978-0-12-800286-5.00005-5.

17. le Roux, A., Snyder-Mackler, N., Roberts, E.K., Beehner, J.C., Bergman, T.J., Beehner, J.C., and Bergman, T.J. (2013). Evidence for Tactical Concealment in a Wild Primate. Nat. Commun. 4, 1462. https://doi.org/10.1038/ ncomms2468.

18. Knott, C.D., Emery Thompson, M., Stumpf, R.M., McIntyre, M.H., and McIntyre, M.H. (2010). Female Reproductive Strategies in Orangutans, Evidence for Female Choice and Counterstrategies to Infanticide in a Species with Frequent Sexual Coercion. Proc. Biol. Sci. 277, 105–113. 1678. https://doi.org/10. 1098/rspb.2009.1552.

19. Fox, E.B. (2002). Female Tactics to Reduce Sexual Harassment in the Sumatran Orangutan (Pongo Pygmaeus Abelii). Behav. Ecol. Sociobiol. 52, 93–101. https://doi.org/ 10.1007/s00265-002-0495-x.

20. Palombit, R.A. (2015). Infanticide as Sexual Conflict: Coevolution of Male Strategies and Female Counterstrategies. Cold Spring Harbor Perspect. Biol. 7, a017640. https://doi.org/ 10.1101/cshperspect . a017640.

21. Palombit, R.A. (1999). Infanticide and the Evolution of Pair Bonds in Nonhuman Primates. Evol. Anthropol. Issues News Rev. 7, 117–129. https://doi.org/10.1002/(SICI)

22. 1520-6505(1999)7: 4<117::AID-EVAN2>3.0. CO;2-O.

22. Snyder-Mackler, N., Burger, J.R., Gaydosh, L., Belsky, D.W., Noppert, G.A., Campos, F.A., Bartolomucci, A., Yang, C., Aiello, A.E., O'Rand, A., et al. (2020). Social Determinants of Health and Survival in Humans and Other Animals. Science 368, 6493. eaax9553. https://doi.org/10.1126/science. aax9553.

23. Seeman, T.E., Singer, B.H., Ryff, C.D., Dienberg Love, G., Levy-Storms, L., and Lené. (2002). Social Relationships, Gender, and Allostatic Load Across Two Age Cohorts. Psychosom. Med. 64, 395–406.

24. Young, C., Majolo, B., Heistermann, M., Schülke, O., and Ostner, J. (2014). Responses to Social and Environmental Stress Are Attenuated by Strong Male Bonds in Wild Macaques. Proc. Natl. Acad. Sci. USA. 111, 18195–18200. https://doi.org/10.1073/pnas. 1411450111.

25. Ostner, J., and Schülke, O. (2018). Linking sociality to fitness in primates: a call for mechanisms. In Advances in the Study of Behavior, 50, M. Naguib, J.C. Mitani, L.W. Simmons, L. Barrett, S.D. Healy, and M. Zuk, eds., Advances in the Study of Behavior (Elsevier), pp. 127–175. https://doi.org/10. 1016/bs.asb.2017.12.001.

26. Waldron, I., Hughes, M.E., and Brooks, T.L. (1996). Marriage Protection and Marriage Selection—Prospective Evidence for Reciprocal Effects of Marital Status and Health. Soc. Sci. Med. 43, 113–123. https:// doi.org/10.1016/0277-9536(95)00347-9.

27. Gardner, J., and Oswald, A. (2004). How Is Mortality Affected by Money, Marriage, and Stress? J. Health Econ. 23, 1181–1207. https:// doi.org/10.1016/j.jhealeco.2004.03.002.

28. Staehelin, K., Schindler, C., Spoerri, A., and Zemp Stutz, E.; Swiss National Cohort Study Group. Zemp Stutz, Elisabeth, and for the Swiss National Cohort Study Group (2012). Marital Status, Living Arrangement and Mortality: Does the Association Vary by Gender? J. Epidemiol. Community Health 66, e22. https://doi.org/10.1136/jech.2010. 128397.

29. Lemasson, A., Palombit, R.A., and Jubin, R. (2008). Friendships between Males and Lactating Females in a Free-Ranging Group of Olive Baboons (Papio Hamadryas Anubis): Evidence from Playback Experiments. Behav. Ecol. Sociobiol. 62, 1027–1035. https://doi. org/10.1007/s00265-007-0530-z.

30. Archie, E.A., Tung, J., Clark, M., Altmann, J., and Alberts, S.C. (2014). Social Affiliation Matters: Both Same-Sex and Opposite-Sex Relationships Predict Survival in Wild Female Baboons. Proc. Biol. Sci. 281, 20141261. 1793. https://doi.org/10.1098/rspb. 2014.1261.

31. Nguyen, N., Van Horn, R.C., Alberts, S.C., Altmann, J., and Altmann, J. (2009). Friendships" between NewMothers and AdultMales: Adaptive Benefits and Determinants inWild Baboons (Papio Cynocephalus). Behav. Ecol. Sociobiol. 63, 1331–1344. 9.

32. Haunhorst, C.B., Heesen, M., Ostner, J., and Schülke, O. (2017). Social Bonds with Males Lower the Costs of Competition for Wild Female Assamese Macaques. Anim. Behav. 125, 51–60. https://doi.org/10.1016/j. anbehav.2017.01.008.

33. Cappozzo, H.L., Túnez, J.I., and Cassini, M.H. (2008). Sexual Harassment and Female Gregariousness in the South American Sea Lion, Otaria Flavescens. Naturwissenschaften

95, 625–630. https://doi.org/10.1007/s00114-008-0363-2.

34. Cameron, E.Z., Setsaas, T.H., and Linklater, W.L. (2009). Social Bonds between Unrelated Females Increase Reproductive Success in Feral Horses. Proc. Natl. Acad. Sci. USA. 106, 13850–13853. https://doi.org/10.1073/pnas. 0900639106.

35. Bro-Jørgensen, J. (2011). Intra- and Intersexual Conflicts and Cooperation in the Evolution of Mating Strategies: Lessons Learnt From Ungulates. Evol. Biol. 38, 28–41. https://doi.org/10.1007/s11692-010- 9105-4.

36. Paoli, T. (2009). The Absence of Sexual Coercion in Bonobos. Sexual coercion in Primates and Humans, 410–423. https://doi. org/10.4159/9780674054349-016.

37. Newton-Fisher, N.E. (2006). Female Coalitions Against Male Aggression in Wild Chimpanzees of the Budongo Forest. Int. J. Primatol. 27, 1589–1599. https://doi.org/10. 1007/s10764-006-9087-3.

38. Charpentier, M.J.E., Huchard, E., Widdig, A., Gimenez, O., Sallé, B., Kappeler, P., and Renoult, J.P. (2012). Distribution of Affiliative Behavior Across Kin Classes and Their Fitness Consequences in Mandrills. Ethology 118, 1198–1207. Ed. by L. Fusani. https://doi.org/ 10.1111/eth.12026.

39. Muller, M.N., Thompson, M.E., and Wrangham, R.W. (2006). Male Chimpanzees Prefer Mating with Old Females. Curr. Biol. 16, 2234–2238. https://doi.org/10.1016/j.cub. 2006.09.042.

40. Mitani, J., Merriwether, D., and Zhang, C. (2000). Male Affiliation, Cooperation and Kinship in Wild Chimpanzees. Anim. Behav. 59, 885–893. https://doi.org/10.1006/anbe. 1999.1389.

41. Gerber, L., Connor, R.C., King, S.L., Allen, S.J., Wittwer, Samuel, Bizzozzero, Manuela, R., Friedman, W.R., Kalberer, S., et al. (2020). Affiliation History and Age Similarity Predict Alliance Formation in Adult Male Bottlenose Dolphins. Behav. Ecol. 31.2, 361–370. Ed. by Michael Taborsky. https://doi.org/10.1093/ beheco/arz195.

42. Gruber, J.E., and Bjorn, L. (1986). Women's Responses to Sexual Harassment: An Analysis of Sociocultural, Organizational and Personal Resource Models. Soc. Sci. Q. 67, 814–826.

43. Folke, O., Rickne, J., Tanaka, S., and Tateishi, Y. (2020). Sexual Harassment of Women Leaders. Daedalus 149, 180–197. https://doi. org/10.1162/daed_a_01781.

44. Dezeure, J., Charpentier, M.J.E., and Huchard, E. (2022). Fitness Effects of Seasonal Birth Timing in a Long-Lived Social Primate Living in the Equatorial Forest. Anim. Behav. 185, 113–126. https://doi.org/10.1016/j. anbehav.2022.01.002.

45. Setchell, J.M., Lee, P.C., Wickings, E.J., and Dixson, A.F. (2001). Growth and Ontogeny of Sexual Size Dimorphism in the Mandrill (Mandrillus Sphinx). Am. J. Phys. Anthropol. 115, 349–360. https://doi.org/10.1002/ ajpa.1091.

46. Setchell, J.M., Charpentier, M., and Wickings, E.J. (2005). Mate Guarding and Paternity in Mandrills: Factors Influencing Alpha Male Monopoly. Anim. Behav. 70, 1105–1120. https://doi.org/10.1016/j.anbehav.2005. 02.021.

47. Smit, N., Baniel, A., Roura-Torres, B., Amblard-Rambert, P., Charpentier, M.J.E., Huchard, E., and Huchard, E. (2022a). Sexual Coercion in a Natural Mandrill Population.

Peer Community J. *2*, e36. https://doi.org/10.24072/pcjournal.134.

48. Brockmeyer, T., Kappeler, P.M., Willaume, E., Benoit, L., Mboumba, S., and Charpentier, M.J.E. (2015). Social Organization and Space Use of a Wild Mandrill (*Mandrillus Sphinx*) Group: Mandrill Social Organization and Space Use. Am. J. Primatol. *77*, 1036–1048. https://doi.org/10.1002/ajp.22439.

49. Smit, N., Ngoubangoye, B., Charpentier, M.J.E., and Huchard, E. (2022b). Dynamics of Intersexual Dominance in a Highly Dimorphic Primate. Front. Ecol. Evol. *10*, 931226. https://doi.org/10.3389/fevo.2022.931226.

50. Charpentier, M.J.E., Peignot, P., Hossaert-McKey, M., and Wickings, E.J. (2007). Kin Discrimination in Juvenile Mandrills, Mandrillus Sphinx. Anim. Behav. *73*, 37–45. https://doi.org/10.1016/j. anbehav.2006.02.026.

51. Charpentier, M.J.E., Harté, M., Poirotte, C., de Bellefon, J.M., Laubi, B., Kappeler, P.M., and Renoult, J.P. (2020). Same Father, Same Face: Deep Learning Reveals Selection for Signaling Kinship in a Wild Primate. Sci. Adv. *6*, eaba3274. 22. https://doi.org/10.1126/sciadv.aba3274.

52. Setchell, J.M., Knapp, L.A., and Wickings, E.J. (2006). Violent Coalitionary Attack by Female Mandrills against an Injured Alpha Male. Am. J. Primatol. *68*, 411–418. https://doi.org/10.1002/ajp.20234.

53. Clarke, P., Pradhan, G., van Schaik, Carel, Muller, M.N., and Wrangham, R.W. (2009). Intersexual conflict in primates: infanticide, paternity allocation, and the role of coercion. In Sexual Coercion in Primates and Humans, M.N. Muller and R.W. Wranham, eds., pp. 42–77.

54. Swedell, L., and Schreier, A. (2009). Male Aggression towards Females in Hamadryas Baboons: Conditioning, Coercion, and Control. In Sexual coercion in Primates and Humans: An Evolutionary Perspective on Male Aggression against Females (Harvard University Press), pp. 244–268. https://doi.org/10.4159/9780674054349- 010.

55. King, S.L., Allen, S.J., Krützen, M., and Connor, R.C. (2019). Vocal Behaviour of Allied Male Dolphins during Cooperative Mate Guarding. Anim. Cogn. *22*, 991–1000. https://doi.org/10.1007/s10071-019-01290-1.

56. Baniel, A., Webb, C.E., Cowlishaw, G., and Huchard, E. (2021). The Submissive Pattern of Postconflict Affiliation in Asymmetric Relationships: A Test in Male and Sexually Coerced Female Baboons. Anim. Behav. *175*, 87–97. https://doi.org/10.1016/j.anbehav.2021.02.014.

57. Palombit, R., Seyfarth, R., and Cheney, D. (1997). The Adaptive Value of 'Friendships' to Female Baboons: Experimental and Observational Evidence. Anim. Behav. *54*, 599–614. https://doi.org/10.1006/anbe.1996.0457.

58. Baniel, A., Cowlishaw, G., and Huchard, E. (2016). Stability and Strength of Male-Female Associations in a Promiscuous Primate Society. Behav. Ecol. Sociobiol. *70*, 761–775. https://doi.org/10.1007/s00265-016-2100-8.

59. Manson, J.H. (1991). Female Mate Choice in Cayo Santiago Rhesus Macaques (University of Michigan).

60. Smuts, B.B. (1985). Sex and Friendship in Baboons (Aldine Publishing Co). https://doi.org/10.4324/9781315129204.

61. Cassini, M.H. (2020). A Mixed Model of the Evolution of Polygyny and Sexual Size Dimorphism in Mammals. Mamm Rev. *50*, 112–120. https://doi.org/10.1111/mam.12171.

62. Emery Thompson, M., and Wrangham, R.W. (2008). Male Mating Interest Varies with Female Fecundity in Pan Troglodytes Schweinfurthii of Kanyawara, Kibale National Park. Int. J. Primatol. *29*, 885–905. https://doi.org/10.1007/s10764-008-9286-1.

63. Hamilton, W.D. (1971). Geometry for the Selfish Herd. J. Theor. Biol. *31*, 295–311. https://doi.org/10.1016/0022-5193(71)90189-5.

64. van Schaik, C.P., Bshary, R., Wagner, G., Cunha, F., and Cunha, F. (2022). Male Anti-Predation Services in Primates as Costly Signalling? A Comparative Analysis and Review. Ethology *128*, 1–14. https://doi.org/10.1111/eth.13233.

65. Cense, M., and Brackenridge, C. (2001). Temporal and Developmental Risk Factors for Sexual Harassment and Abuse in Sport. Eur. Phys. Educ. Rev. *7*, 61–79. https://doi.org/10.1177/1356336X010071006.

66. Kalbitzer, U., Bergstrom, M.L., Carnegie, S.D., Wikberg, E.C., Kawamura, S., Campos, F.A., Jack, K.M., and Fedigan, L.M. (2017). Female Sociality and Sexual Conflict Shape Offspring Survival in a Neotropical Primate. Proc. Natl. Acad. Sci. USA. *114*, 1892–1897. https://doi.org/10.1073/pnas.1608625114.

67. Dinh, T., Gangestad, S.W., Thompson, M.E., Tomiyama, A.J., Fessler, D.M.T., Robertson, T.E., Haselton, M.G., and Haselton, M.G. (2021). Endocrinological Effects of Social Exclusion and Inclusion: Experimental Evidence for Adaptive Regulation of Female Fecundity. Horm. Behav. *130*, 104934. https://doi.org/10.1016/j.yhbeh.2021.104934.

68. Tuncgenc, B., van Mulukom, V., and Newson, M. (2023). Social Bonds Are Related to Health Behaviors and Positive Well-Being Globally. Sci. Adv. *9*, eadd3715. https://doi.org/10.1126/sciadv . add3715.

69. Menz, C.S., Carter, A.J., Best, E.C., Freeman, N.J., Dwyer, R.G., Blomberg, S.P., and Goldizen, A.W. (2020). "Higher Sociability Leads to Lower Reproductive Success in Female Kangaroos". R. Soc. Open Sci. *7*, 200950. https://doi.org/10.1098/rsos.200950.

70. Blumstein, D.T., Williams, D.M., Lim, A.N., Kroeger, S., and Martin, J.G.A. (2018). Strong Social Relationships Are Associated with Decreased Longevity in a Facultatively Social Mammal. Proc. Biol. Sci. *285*, 20171934. https://doi.org/10.1098/rspb. 2017.1934.

71. Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A.M., Agil, M., Widdig, A., and Engelhardt, A. (2011). Assessing Dominance Hierarchies: Validation and Advantages of Progressive Evaluation with Elo-rating. Anim. Behav. *82*, 911–921. https://doi.org/10.1016/j. anbehav.2011.07.016.

72. Csardi, G., and Nepusz, T. (2006). The Igraph Software Package for Complex Network Research (InterJournal Complex Systems), p. 1695.

73. Brooks, M.E., Kristensen, K., Benthem, K., Magnusson, A., Berg, C., Nielsen, A., Skaug, H., Mächler, M., Bolker, B., and Bolker, B.M. (2017). glmmTMB Balances Speed and Flexibility among Packages for Zero-Inflated Generalized Linear Mixed Modeling. The R Journal *9*, 378–400.

74. Fox, J. and Weisberg, S. (2019). An R Companion to Applied Regression. Third. Thousand Oaks CA: Sage.

75. Hartig, F. (2022). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/ Mixed) Regression Models. Manual.

76. Wickham, Hadley, C. W. H., Lionel, P., T. Lin, Kohske, W, Claus, W., Kara, Y, Hiroaki, D., Dewey, Posit, and PBC (2023). Ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics.

77. Peignot, P., Charpentier, M.J., Bout, N., Bourry, O., Massima, U., Dosimont, O., Terramorsi, R., and Wickings, E.J. (2008). Learning from the First Release Project of Captive-Bred Mandrills Mandrillus Sphinx in Gabon. Oryx *42*. 01. https://doi.org/10.1017/S0030605308000136.

78. David, H.A. (1987). Ranking from Unbalanced Paired-Comparison Data. Biometrika *74*, 432–436. https://doi.org/10.1093/biomet/74.2.432.

79. Galbany, J., Romero, A., Mayo-Alesón, M., Itsoma, F., Gamarra, B., Pérez-Pérez, A., Kappeler, P.M., Charpentier, M.J.E., Eric, et al.. (2014). Age-Related Tooth Wear Differs between Forest and Savanna Primates. PLoS One *9*, e94938. https://doi.org/10.1371/journal.pone.0094938.

80. Siracusa, E.R., Negron-Del Valle, Josué, E., Phillips, D., Platt, M.L., Higham, J.P., Snyder-Mackler, N., and Brent, L.J.N. (2022). Within-Individual Changes Reveal Increasing Social Selectivity with Age in Rhesus Macaques. Proc. Natl. Acad. Sci. USA *119*, e2209180119. 49. https://doi.org/10.1073/pnas.2209180119.

81. Setchell, J.M., Lee, P.C., Wickings, E.J., and Dixson, A.F. (2002). Reproductive Parameters and Maternal Investment in Mandrills (Mandrillus Sphinx). Int. J. Primatol. *18*. https://doi.org/10.1023/A:1013245707228.

82. Campos, F.A., Altmann, J., Cords, M., Fedigan, L.M., Lawler, R., Lonsdorf, E.V., Stoinski, T.S., Strier, K.B., Bronikowski, A.M., Pusey, A.E., and Alberts, S.C. (2022). Female Reproductive Aging in Seven Primate Species: Patterns and Consequences. Proc. Natl. Acad. Sci. USA. *119*, e2117669119. https://doi.org/10.1073/pnas.2117669119.

83. Seyfarth, R.M., and Cheney, D.L. (2012). The Evolutionary Origins of Friendship. Annu. Rev. Psychol. *63*, 153–177. https://doi.org/10.1146/annurev-psych-120710-100337.

84. Wey, T.W., Burger, J.R., Ebensperger, L.A., and Hayes, L.D. (2013). Reproductive Correlates of Social Network Variation in Plurally Breeding Degus (Octodon Degus). Anim. Behav. *85*, 1407–1414. https://doi.org/10.1016/j.anbehav.2013.03.035.

85. Beaulieu, M., Benoit, L., Abaga, S., Kappeler, P.M., and Charpentier, M.J.E. (2017). Mind the Cell: Seasonal Variation in Telomere Length Mirrors Changes in Leucocyte Profile. Mol. Ecol. *26*, 5603–5613. https://doi.org/10.1111/mec.14329.

86. Ramos-Fernández, G., Boyer, D., Aureli, F., and Vick, L.G. (2009). Association Networks in Spider Monkeys (Ateles Geoffroyi). Behav. Ecol. Sociobiol. *63*, 999–1013. https://doi.org/10.1007/s00265-009-0719-4.

87. Bonacich, P. (2007). Some Unique Properties of Eigenvector Centrality. Soc. Network. *29*, 555–564. https://doi.org/10.1016/j.socnet.2007.04.002.

88. Ruhnau, B. (2000). Eigenvector-Centrality — a Node-Centrality? Soc. Network. *9*, 357–365.

89. Seyfarth, R.M., and Cheney, D.L. (1984). Grooming, Alliances and Reciprocal Altruism in Vervet Monkeys. Nature *308*, 541–543. https://doi.org/10.1038/308541a0.

90. Ventura, R., Majolo, B., Koyama, N.F., Hardie, S., and Schino, G. (2006). Reciprocation and

Interchange in Wild Japanese Macaques: Grooming, Cofeeding, and Agonistic Support. Am. J. Primatol. *68*, 1138–1149. https://doi.org/10.1002/ajp.20314.

91. Vander Wal, E., Festa-Bianchet, M., Réale, D., Coltman, D.W., and Pelletier, F. (2015). Sex-Based Differences in the Adaptive Value of Social Behavior Contrasted against Morphology and Environment. Ecology *96*, 631–641. https://doi.org/10.1890/14-1320.1.

92. Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M., and Cheney, D.L. (2010). Strong and Consistent Social Bonds Enhance the Longevity of Female Baboons. Curr. Biol. *20*, 1359–1361. https://doi.org/10.1016/j.cub.2010.05.067.

93. Team, R Developement Core (2010). "R: A Language and Environment for Statistical Computing".

94. Tinsley Johnson, E., Snyder-Mackler, N., Beehner, J.C., Bergman, T.J., and Bergman, T.J. (2014). Kinship and Dominance Rank Influence the Strength of Social Bonds in Female Geladas (Theropithecus Gelada). Int. J. Primatol. *35*, 288–304. https://doi.org/10.1007/s10764-013-9733-5.

95. Bray, J., Feldblum, J.T., and Gilby, I.C. (2021). Social Bonds Predict Dominance Trajectories in Adult Male Chimpanzees. Anim. Behav. *179*, 339–354. https://doi.org/10.1016/j.anbehav.2021.06.031.

96. Schülke, O., Bhagavatula, J., Vigilant, L., and Ostner, J. (2010). Social Bonds Enhance Reproductive Success in Male Macaques.

Curr. Biol. *20*, 2207–2210. https://doi.org/10.1016/j.cub.2010.10.058.

97. Kenny, D.A., Kashy, D.A., Bolger, N., Gilbert, D., Fiske, S.T., and Lindzey, G. (1998). Data analysis in social psychology. In The Handbook of Social Psychology, 4th edition, D. Gilbert, S. Fiske, and G. Lindzey, eds. (McGraw-Hill), pp. 233–265.

98. Steiger, J.H. (2007). Understanding the Limitations of Global Fit Assessment in Structural Equation Modeling. Pers. Indiv. Differ. *42*, 893–898. https://doi.org/10.1016/j.paid.2006.09.017.

99. Rosseel, Y. (2012). Lavaan: An R Package for Structural Equation Modeling. J. Stat. Softw. *48*, 1–36. https://doi.org/10.18637/jss.v048.i02.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Cleaned data and code	GitLab	https://gitlab.com/nksmt/mandrills3
Experimental models: Organisms/strains		
51 female and 39 male free-ranging mandrills	Not applicable	Not applicable
Software and algorithms		
R	R Core Team 2022	https://cran.r-project.org/
R package EloRating	Neumann et al.[71]	https://cran.r-project.org/web/packages/EloRating/
R package igraph	Csardi & Nepusz[72]	https://cran.r-project.org/web/packages/igraph/
R package glmmTMB	Brooks et al.[73]	https://cran.r-project.org/web/packages/glmmTMB/
R package car	Fox[74]	https://cran.r-project.org/web/packages/car/
R package DHARMa	Florian[75]	https://cran.r-project.org/web/packages/DHARMa/
R package lavaan	Rosseel et al.	https://cran.r-project.org/web/packages/lavaan/
R package ggplot2	Wickham et al.[76]	https://cran.r-project.org/web/packages/ggplot2/
TikZ (TeX)	The TikZ and PGF Packages	https://www.ctan.org/pkg/pgf

RESOURCE AVAILABILITY

Lead contact

Further information should be directed to and will be fulfilled by the lead contact, Nikolaos Smit (snikos@tutanota.com).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- Data are available at https://gitlab.com/nksmt/mandrills3
- All original code has been deposited at https://gitlab.com/nksmt/mandrills3
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Ethical guidelines

This study was approved by an authorization from the CENAREST institute (permit number, AR017/22/MESRSTTCA/ CENAREST/CG/CST/ CSAR) and followed all applicable international, national, and/or institutional guidelines for the care and use of animals.

Study population

We studied a natural population of unfed, non-manipulated mandrills that range freely in the surroundings of Lékédi Park, in Southern Gabon. The social group was initially founded by captive mandrills from CIRMF (Centre International de Recherches Médicales de Franceville, Gabon) released on two occasions, in 2002 and 2006.[77] The study group is habituated to human presence and daily observations are performed within the framework of the Mandrillus Project, established in 2012 to study mandrills' life-history, ecology and behaviour. In late 2021, the group consisted of c.a. 220 individuals including only 7 females born in captivity (for more details on the origins of the group see[48]). We used behavioural and life-history data from 2012-2021, excluding 2020 due to COVID19 pandemic-related disruptions, for a total of 51 adult females aged 4 yrs and older, and 39 subadult and adult males aged 9 yrs and older.[45] We considered the mating season to occur from April 1st to September 30th and the rest of the year to correspond to the birth season.[44]

METHOD DETAILS

Behavioral observations

Observers blind to the topic of this study conducted daily *ad libitum* behavioural observations and 5-min focal sampling on individually-recognized males and females. We considered a total of 24169 focal observations (18767 and 5402 on females and males, corresponding to 1564 and 450 hours, respectively). During focal observations, agonistic (aggressive: grasping/hitting, biting, chasing, lunging, slapping the ground and head bobbing; submissive: avoidance, displacement, escape and submissive vocalization) and grooming interactions were recorded along with other behaviours. These observations were interspersed with up to three proximity scans (every 2 minutes approximately) recording the identities of all individuals located within 5m from the focal individual.

Individual traits

Dominance ranks

We used the function *DS* from the R package *EloRating* version 0.46.11[71] to compute intersexual hierarchies based on submissive dyadic interactions that were recorded between and within the sexes during focal or *ad libitum* observations, as per.[49] This function produces individual David's scores[78] using the proportion of wins of each individual in each dyad (corrected for the number of agonistic interactions; prop="Dij"). Differences between individual scores correspond to dominance asymmetries, calculated for each female-male dyad. Previous results have shown that higher-ranking female mandrills receive significantly more male aggression and that higher-ranking males are more coercive.[47] In our models described below we therefore used both female and male rank as control variables, retrieved from the intersexual hierarchy (based on both within and between-sex interactions) because high-ranking females occasionally outrank some males.[49]

Age

The exact birth date was known for 21 individuals. For the remaining 69 individuals, we estimated age based on body condition and patterns of tooth wear and eruption.[79] For 37 individuals the estimation uncertainty was < 1 year and for 32 individuals it was 1-3 years. We controlled for both male and female ages because age may impact social relationships in primates.[80] In addition, we considered the quadratic term of female age because mid-aged females might be more attractive due to their higher fertility or reproductive success than young or old females,[81,82] possibly influencing male coercive behaviours.

Reproductive state and reproductive success

Observers recorded the reproductive state of each sexually mature female on a near-daily basis. During estrus periods, which mostly occur during the mating season, females exhibit sexual swellings which gradually inflate (recorded on a scale from 0 to 3 by increments of 0.5[44]) until reaching a maximal size, around ovulation, before deflating. Here, we considered only estrus cycles that ended with a conception and calculated male aggression from the beginning of the mating season until the beginning of this cycle in order to include all the episodes of sexual receptivity in case a female had more than one estrus cycle within a mating season before conceiving. The exact number of estrus cycles is hard to document in mandrills because a female's sexual swelling might inflate and deflate several times before conception without always reaching maximum size or deflating completely.

We calculated the number of surviving offspring (surviving > 6 months; see[44]) that a female had until each mating season, as a proxy of female reproductive success in our path analysis.

Matriline size

For each female, we calculated matriline size as the number of adult females with whom she was sharing a common mother or a common maternal grand-mother present in the group at the beginning of each mating season. Maternally related females who were released on two different occasions from CIRMF (in 2002 vs 2006) were considered as belonging to two distinct matrilines due to major social disruptions affecting the female social structure and hierarchical relationships. In particular, all females released in 2006 ended-up in a lower hierarchical position than those released in 2002 (MJEC unpublished data).

Sex ratio

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

QUANTIFICATION AND STATISTICAL ANALYSIS

Quantifying sexual coercion

Following previous results on sexual coercion in mandrills, we calculated sexual coercion, for each female-male dyad and each mating season, as the total number of male aggressive events towards the female recorded during a period starting at the male's arrival in the group that year

(for immigrant males) or at the arrival of the first immigrant male in the group that year (for resident males) and ending on the first day of the swelling phase of a female's estrus cycle.[47] Although all male-to-female aggression events during this period might not reflect exclusively sexual coercion, we grouped them under the term 'sexual coercion' throughout the manuscript because of their correlation with male mating success.[47] Conversely, we did not consider male-to-female aggression during the swelling phase as sexual coercion because it did not correlate with male mating success[47] and thus, did not fall within the definition of sexual coercion.[5] For each mating season, we considered as residents those males who were censused in the group in the three months preceding that mating season (January-March), and as immigrants those who were first censused that mating season (April-September). In addition, and for each estrus cycle, we calculated the coercion a female received from all males as the total number of aggressive events she received from them between the onset of the mating season and first day of the swelling phase of her estrus cycle. A female received aggression on average 0.83 ± 1.40 ($\pm$SD) times per hour of observation. We included both severe (grasping/hitting, biting, chasing; in 35 out of 801 dyad.years) and mild (lunging, slapping the ground, head bobbing; in 79 out of 801 dyad.years) aggressive events because they both increase male mating success.[47] A female received aggression from a given male a maximum of five times (two cases) and on average she received aggression 0.04 ± 0.20 ($\pm$SD) times per hour of observation.

Quantifying social bonds

Female-male bonds (heterosexual networks)

For each female-male dyad, we calculated scores of grooming (total duration of grooming recorded during focal observations divided by the total focal observation time of both members of the dyad) and proximity (number of scans a dyad was recorded in spatial proximity divided by the total number of scans collected from both members of the dyad), from the arrival of the male in the group (for immigrant males) or the onset of the mating season (for resident males) until the beginning of the female's estrus cycle. We included only grooming given by the female to the male because male mandrills rarely groom females and we considered female grooming effort to represent the investment in maintaining a bond with a given male. We observed female-to-male grooming in 73 out of 801 dyad.years. In an average dyad the female groomed the male for 0.04 ± 0.28 mins ($\pm$SD) per hour of observation. For each female, we also determined her 'top male partner', either as the male she groomed the most or as the one with whom she was most often in spatial proximity, from the beginning of the mating season to her first estrus day. A female groomed her top grooming male partner for 0.38 ± 0.94 mins ($\pm$SD) per hour of observation. In most cases, except two, this male was present in the group for the whole duration of the sampling period. The resolution of our records of males supporting females against other males, or males directing aggression to rivals who have previously directed aggression to females did not allow any quantitative analyses.

We constructed two separate heterosexual social networks based on (i) grooming interactions and (ii) spatial proximity; grooming may better reflect affiliative bonds, while proximity may instead reflect females coming close to certain males when they are threatened by other males. The edges (connections) among adjacent individuals were weighted either by grooming or proximity scores of the heterosexual dyads. For each network, we calculated a female's strength as the sum of weights of her edges. We constructed one heterosexual social network for each estrus cycle of each female because networks may differ across seasons.

Female-female bonds (female-only networks)

We constructed female social networks including only grooming interactions because in many primates, grooming partners are likely to support each other during coalitions against conspecifics of either sex.[83] A female was observed grooming with another female on average 4.91 ± 5.35 mins ($\pm$SD) per hour of observation. For each mating season, we constructed a network using data from the three last months of the preceding birth season (January-March), for two main reasons. First, female social interactions recorded just before the arrival of immigrant males are more likely to reflect the social landscape that these males face when entering the group and making decisions such as choosing which female to target. Second, the birth season may be more appropriate to measure stable patterns of female-female social bonds, independently of the stress and disruptions generated by sexual interactions, male-male competition, and male hierarchical instability in the mating season[83,84] (for mandrills see also[85]).

We used two classical social network metrics to measure a female's position in the female-only network: eigenvector centrality and strength.[86] First, eigenvector centrality is a proxy of individual connectivity that takes into account indirect connections (i.e. connections mediated by third parties) by weighing every connection according to the centrality of the relevant adjacent individuals.[87] An individual has a higher value of eigenvector centrality if connected to more central individuals.[88] Second, female strength was computed as the total grooming she gave to, or received from, other female groupmates (sum of all inward and outward edge weights in grooming networks) because in contrast to between-sex grooming interactions, female mandrills may offer grooming to each other and may support both the one to whom they give[89] or from whom they receive[90] grooming. High values of both eigenvector centrality and grooming strength in other species have been associated with higher female fitness.[91,92]

We used the function *graph_from_data_frame* to create grooming and proximity networks and the functions *centr_eigen* and *strength* to compute eigenvector centrality and strength of each individual, respectively (R package *igraph* version 1.4.1[72]). Finally, we used TikZ (TeX) and the R package *ggplot2*[76] to visualize our results.

Statistical analyses

We first investigated the correlation structure of the different individual variables (age, rank, social variables) using pairwise Spearman's rank correlations to clarify which variables may fit together in multivariate models. Higher-ranking females had, on average, larger matrilines (rho=0.36, p-value < 0.001) than lower-ranking females, but female rank was not correlated with any other proxy of female-female social bonds (not shown). Females with higher eigenvector centrality also had higher strength in the female-only network (rho=0.5, p-value < 0.001), suggesting that these two metrics might capture similar social dynamics. Therefore, we did not include them in the same model. All other pairwise correlations were non-significant.

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

We ran two GLMMs with negative binomial distributions to examine the determinants of variation in sexual coercion across female-male dyads (response variable: number of aggressive events received by the female from a given male). We considered the dyad observation time (log-transformed) as an offset variable. We included the following explanatory variables: grooming score of the heterosexual dyad during the period over which coercion was recorded, the difference between male and female David's scores, male and female age and their quadratic terms, and the operational sex-ratio. We included female and male identity as well as the year of observation as random factors. We then re-ran this model including the proximity score of the heterosexual dyad, instead of the grooming score, due to the correlation of these two scores (Spearman's rank correlation test: rho=0.38, p-value < 0.001). Finally, we also ran the above model changing some parameters in order to verify the robustness of our results. First, we re-ran our analysis including male-to-female aggression during the swelling phase of a female's estrous cycle (response variable: number of aggressive events received by the female from a given male from his arrival in the group until the end of the swelling phase of the female's estrous cycle). Second, although in our analyses we included all dyads, regardless of their observation time, we repeated the analysis including only dyads observed for at least 20, 30, 45 or 60 mins. In all cases, our results remained qualitatively similar to those presented above.

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

We ran two GLMMs with negative binomial distributions to study the effects of female-male social bonds on the overall sexual coercion a female faces. First, we tested whether the intensity of sexual coercion faced by a female (response variable: number of aggression events received by a female from all males except her top grooming partner) was associated to her out-strength with her top male grooming partner in the grooming network. We considered female observation time (log-transformed) as an offset variable. We also included the following control variables: female dominance rank, top male partner's rank (in case male rank influences the ability to protect his female partner), female age (and its quadratic term) and operational sex-ratio. We included female identity and the year of observation as random factors. We then re-ran this model calculating both the response variable (coercion) and explanatory variables based on the top male proximity partner rather than on the top male grooming partner.

Does female integration in the female-only network or the number of maternal kin in the group protect her against male coercion (P3)?

We ran three GLMMs with negative binomial distributions to study the effects of female-female social integration on the extent of sexual coercion a female receives from all males (response variable: number of aggression events faced by a female from all males before her estrus cycle). We used as the main explanatory variable a female's eigenvector centrality in a first version of the model, and replaced it by female's strength in a second version, and by matriline size in a last version. Otherwise, the structure of control variables (female rank, age and operational sex-ratio), random effects and the offset variable were similar to the models described above.

We used R version 4.1.3[93] to run the above models with the function *glmmTMB* from the package *glmmTMB* version 1.1.6.[73] We tested the significance of all fixed factors with the function *Anova* from package *car* version 3.1.1[74] and we computed their 95% confidence intervals. We tested for multicollinearities with the function *cor.test* and we validated the models by testing the residual distributions, using the functions *testDispersion* and *testUniformity* from package *DHARMa* version 0.4.6.[75]

Is the effect of female-female bonds on sexual coercion direct, or indirectly mediated by female reproductive success or retaliation potential?

We ran a mediation (path) analysis to test if females with high eigenvector centrality in the female-only network face more male coercion because they reproduce successfully ('reproductive success indirect path') and/or they are more powerful ('retaliation indirect path') or simply because they are more exposed to interactions with coercive males ('public exposure direct path'; Figure 2D solid lines). Under the first scenario, because male mandrills are not permanent residents, they may be unable to know a female's past reproductive history and may thus infer it from females' social environment, targeting females who are associated with infants and juveniles. In the second case, we approximate female retaliation potential by her dominance rank in the intersexual hierarchy. This is based on results ranking certain females over some males in the intersexual hierarchy and on occasional observations of females chasing away males. Similarly to other primates,[94–96] the three main variables in our path analysis (reproductive success, dominance rank and social bonds) are largely intertwined in mandrills[38,49] and this path analysis aimed to overcome potential multicollinearities and disentangle the effects of these variables on sexual coercion. The rank of the female in the intersexual hierarchy and her reproductive success were not correlated (Spearman's rank correlation test: rho=0.09,

p-value=0.387). We thus tested both variables simultaneously as potential mediators.[97] In the same analysis, we specified, as above, female age and operational sex ratio as control predictor variables. The root-mean-square error of approximation (RMSEA) was ≤ 0.05, the chi-square test was non-significant (p-value=0.424), the Comparative Fit Index was equal to 1.00 and the Tucker-Lewis Index was equal to 1.064, overall indicating good fit of the analysis.[98] We used R package *lavaan* version 0.6.15[99] for the path analysis.

Finally, following results obtained from the path analysis supporting the 'public exposure' hypothesis, we also ran a similar GLMM to those described in P3, replacing a female's eigenvector centrality with her strength in the heterosexual proximity network, in order to study if overall proximity to males increases the probability of facing male coercion (response variable: number of aggression events faced by a female from all males before her estrus cycle). Otherwise, the structure of control variables (female rank, age and operational sex-ratio), random effects and the offset variable were similar to the models in P3.