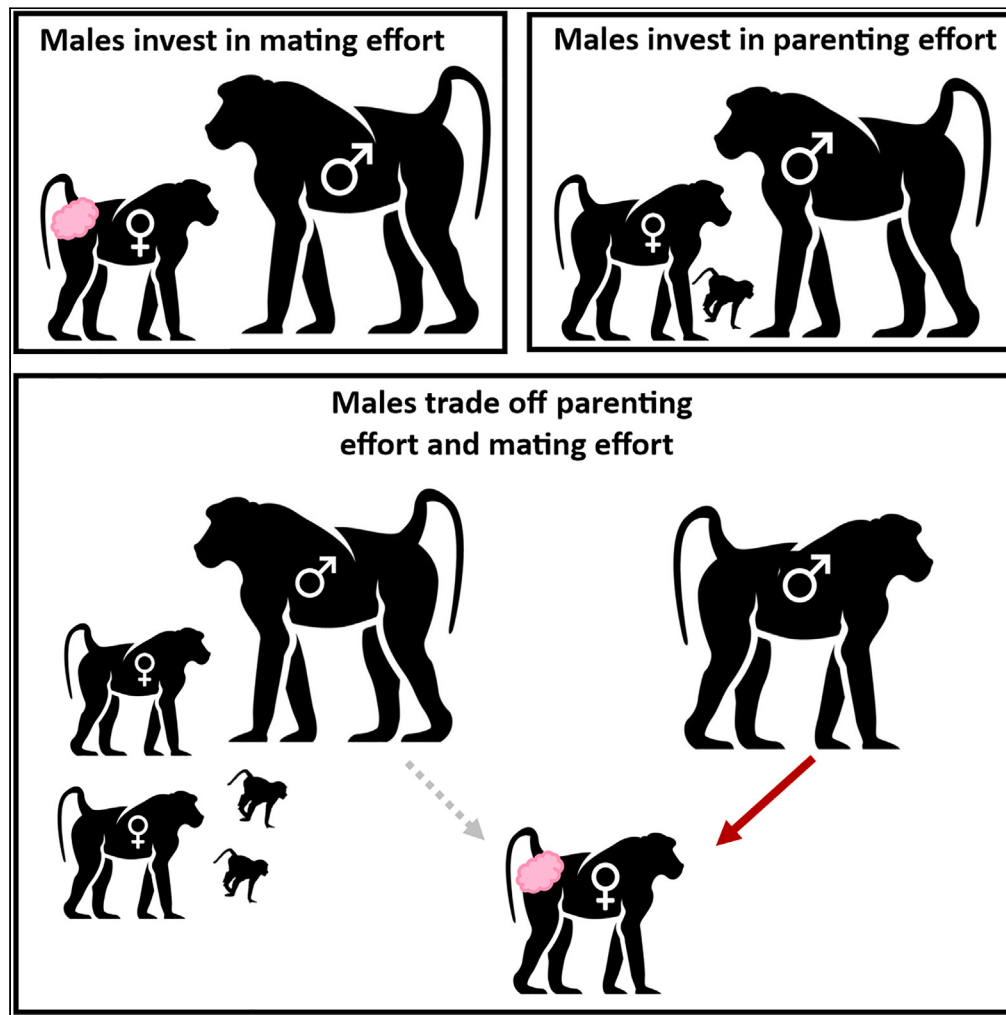


Article

Tradeoffs between mating effort and parenting effort in a polygynandrous mammal



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Highlights

Male olive baboons invest in both mating effort and parenting effort

Investment in parenting effort and mating effort are negatively correlated

Parenting effort has negative, but uncertain, effects on paternity success

Males seem to trade off mating effort and parenting effort

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Article

Tradeoffs between mating effort and parenting effort in a polygynandrous mammal

Caitlin R. Hawley,¹ Sam K. Patterson,² and Joan B. Silk^{1,3,4,*}

SUMMARY

Reproductive strategies are defined by expenditures of time and energy devoted to mating effort, which increases mating opportunities, and parenting effort, which enhances the survival of offspring. We examine tradeoffs between mating effort and parenting effort in male olive baboons, *Papio anubis*, a species in which males compete for mating opportunities, but also form ties to lactating females (primary associations) that represent a form of parenting effort. Males that are involved in more primary associations invest less in mating effort than males who are involved in fewer primary associations. Males that are involved in more primary associations play a smaller role in establishing proximity to their primary associates than other males, suggesting that males operate under temporal constraints. There is also some evidence that involvement in primary associations negatively affects paternity success. Taken together, the data suggest that males face tradeoffs between mating effort and parenting effort.

INTRODUCTION

Male reproductive strategies are defined by expenditures of time and energy devoted to mating effort, which increases mating opportunities, and parenting effort, which enhances the welfare and survival of offspring.¹ There are some circumstances in which mating effort and parenting effort are synergistic.² For example, in glass frogs (*Hyalinobatrachium cappellei*) and harvestmen spiders (*Zygopachylus* spp), females preferentially mate with males that are already caring for a brood.^{3,4} In species that form stable pair bonds or breed cooperatively, the distinction between mating effort and parenting effort is blurred because male parental care may enhance offspring fitness and may also increase female fertility and increase male mating opportunities.⁵ Some forms of male care, such as protection of immatures from predation or infanticide, may be facilitated by the same proximate mechanisms that facilitate male-male competition, such as high levels of testosterone.^{6,7} However, there are also many situations in which mating effort and parenting effort are incompatible, forcing males to make tradeoffs between mating effort and parenting effort.^{7,8} In cooperatively breeding superb fairy wrens (*Malurus cyaneus*), dominant males with helpers spend less time feeding nestlings and more time courting females in neighboring territories than males without helpers do.⁹ In many taxa, there is a negative relationship between testosterone levels and male parenting behavior,¹⁰ suggesting that the hormonal substrates underlying mating effort and parenting effort may not always be compatible.

Tradeoffs between male mating effort and male parenting effort are likely to arise in species with polygynous and polygynandrous mating systems. In these species, sexual selection generally favors increased investment in traits that enhance males' success in male-male competition, including large body size, weaponry, or success in sperm competition.^{11,12} When sexual selection acts more strongly on males than females, males are expected to gain greater fitness benefits from investments in mating effort than parenting effort.^{13,14} In line with theory, male parental care is generally limited in mammalian species with polygynous and polygynandrous mating systems.¹⁵ There are some conspicuous exceptions to this pattern. For example, male mountain gorillas (*Gorilla beringei*) form lasting ties to particular immatures, and protect them from infanticide and harassment.^{16,17} Males that are most active in caring for immatures have the highest reproductive success,¹⁸ but care is not selectively directed toward genetic offspring.¹⁶ Thus, it is not clear whether male care represents a form of mating effort or parenting effort.

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In several species of baboons (genus *Papio*), males compete over access to females and also provide some forms of care for offspring. Yellow (*Papio cynocephalus*), olive (*Papio anubis*), chacma (*Papio ursinus*), and kinda (*Papio kindae*) baboons form large single-level groups and have polygynandrous mating systems.¹⁹ Males weigh 1.6–1.8 times more than females and their canines are 2.0–3.14 times larger than females' canines.²⁰ Yellow, olive, and chacma baboon males compete vigorously for high-ranking positions within their groups, and high-ranking males sire more offspring than low-ranking males do.^{21–23} Males in these species also mate guard sexually receptive females, and mate guarding reduces male foraging time²⁴ and increases male glucocorticoid levels.²⁵ High-ranking yellow baboon males have higher levels of gene expression at loci associated with inflammation, accelerated epigenetic aging, elevated glucocorticoid and testosterone levels, and die at earlier ages than lower ranking males.^{26–28}

Male yellow, olive, chacma, and kinda baboons also form close relationships (primary associations, hereafter) with particular pregnant and lactating females.^{29–32} Several lines of evidence suggest that these relationships represent a form of male parental care. Most importantly, yellow, olive, and chacma males are often the sires of their primary associates' infants.^{22,23,33,34} Males greet, inspect, hold, and carry their primary associates' infants much more than the infants of other females.³⁵ In playback experiments, male chacma and olive baboons respond more strongly to the distress calls of their lactating primary associates than to the calls of other females,^{31,36} but chacma males' responsiveness to females' distress drops if their infants dies.³¹

Primary associations also establish the foundation for lasting relationships between males and maturing offspring.^{37–40} Males selectively support their infant and juvenile offspring and the offspring of their primary associates when they are involved in conflicts.^{39,41} Males also provide their offspring with access to valuable resources,⁴⁰ and enable them to feed more efficiently.⁴² It is not clear how costly these forms of care are to males. However, male chacma baboons that are involved in primary associations experience greater increases in glucocorticoid levels than other males when infanticide risk is elevated by the arrival of new males or instability in the male dominance hierarchy.^{25,43}

It was once thought that primary associations with lactating female baboons represent a form of male mating effort because females would selectively mate with males that had previously provided support for them and their offspring.⁴⁴ However, genetic analyses of paternity in yellow, olive, and chacma baboons indicate that males that form primary associations with lactating females do not increase their chances of siring their primary associates' next offspring.^{22,33,45} After female olive baboons wean their infants and resume cycling, the strength of their ties to their primary associates does not predict the likelihood that their primary associates will sire their next offspring. In contrast, the strength of cycling females' ties to other males does predict the likelihood of paternity.²² Taken together, these data suggest that primary associations are more likely to be a form of male parenting effort than mating effort.

Indirect evidence suggests that male baboons in single-level societies may experience tradeoffs between mating effort and parenting effort. Male yellow and olive baboons are most likely to hold high rank and sire infants in early adulthood when they are in prime physical condition.^{21,35} Testosterone levels are negatively correlated with male dominance rank and male age,²⁸ suggesting a shift in reproductive priorities or capacities as males age. In olive baboons, older males are more likely to form primary associations than younger males, when paternity is held constant.^{35,46} Age-related changes in the payoffs derived from mating effort and parenting effort may favor changes in male reproductive tactics if males face tradeoffs between mating effort and parenting effort.

Here, we consider whether male olive baboons make tradeoffs between mating effort and parenting effort. If males make such tradeoffs, then males that are involved in more primary associations at a given time are expected to allocate less effort to gaining access to sexually receptive females than males that are involved in fewer primary associations. As a consequence, males that are involved in more primary associations are expected to sire fewer offspring than males that are involved in fewer primary associations. To gain insight about whether tradeoffs between mating effort and parenting effort reflect constraints on males' ability to invest in both mating and parenting effort, we also examined the dynamics of males' relationships with their primary associates. If males face constraints on their time or energy, then males that have more primary associates at a given time are expected to play a smaller role in establishing proximity to their primary associates than males who are involved in fewer primary associations.

RESULTS

We studied two groups of wild olive baboons in central Kenya over a three-year period. We conducted 545 h of focal observations on a total of 21 adult and subadult males and recorded their interactions with cycling, pregnant, and lactating females in their groups.

Measurement of male mating effort

To assess male mating effort, we focused on males' approaches to fully swollen females. Female baboons have conspicuous sexual swellings, and are most likely to conceive when their sex skins are fully swollen.^{47–49} Males are strongly attracted to fully swollen females,^{50–54} and their association with fully swollen females during their conception cycles is a strong predictor of paternity in yellow and olive baboons.^{22,37,41} Previous analyses of data from our study groups indicate that the rate of approaches to conceiving females is a strong predictor of paternity,³⁷ but did not account for the potentially confounding effects of male dominance rank.

To assess the validity of the rate of approaches as a measure of male mating effort, we modeled the effects of male dominance rank and the rate of approaches to fully swollen females during their conception cycles (conceiving females, hereafter) on paternity success. We tabulated the number of approaches each male made to each conceiving female (movement to within a 1-m radius) on each day that males were observed. This analysis was based on a sample of 430 male days during 29 conception periods (involving 20 different conceiving females). The relationship between male dominance rank and the rate of approaches to conceiving females was relatively weak ($r = 0.1065$), so it was possible to include both variables in the model. We use the rate of approaches to conceiving females rather than a binary measure of male mate guarding for two reasons. First, it provides a systematic, quantitative measure of male behavior. Second, male mating effort might extend beyond mate-guarding pairs as sexually receptive females are sometimes followed by a phalanx of males that may take advantage of opportunities to mate.⁵⁵

As expected based on previous work, high-ranking males had a higher probability of siring offspring than lower ranking males did (Figure 1A, Table 1). In addition, the model also shows that males that approached conceiving females at higher rates had a higher probability of siring their offspring than males that approached at lower rates (Figure 1B). The inclusion of an interaction between male dominance rank and the rate of approaches to conceiving females did not improve model fit, and this term was omitted from the final model.

Male involvement in primary associations

To assess the extent of male involvement in parenting effort, we tabulated the number of primary associates that each male had on each day that he was observed. Following previous work, focal observations of lactating females were used to identify primary associations.^{22,35,37} For each lactating female, we tabulated the frequency of her interactions with each of the males in her group and computed the Dyadic Sociality Index (DSI) which is a composite normalized score assessing the strength of a dyadic relationship.⁵⁶ For each female in each lactation period, the male with the highest DSI score was considered the primary associate. In some cases, two males had almost identical DSI scores, and both were identified as primary associates.

For each male, we tabulated the number of primary associations that he was involved in on each day. In this population, primary associations emerge during pregnancy and last through lactation,²² so primary associations were assumed to begin on the day that the primary associate became pregnant and end on the day when she resumed cycling or the infant died. The number of primary associates that a male had could change from one day to another as the reproductive status of females changed.

Sixteen of the 21 males were involved in at least one primary association over the course of the study. Males were involved in about one primary association each day on average, but some males were involved in as many as five primary associations on a given day (ENK: 1.35 ± 1.35 , range 0–5; PHG: 0.95 ± 1.03 , range 0–5).

Association between male mating effort and involvement in primary associations

Males who had more primary associates on a given day approached fully swollen females less often than males that had fewer primary associates, when rank is held constant. As the number of primary associations that a male was involved in increased, the median value of the predictive probability distribution of the rate of approaches

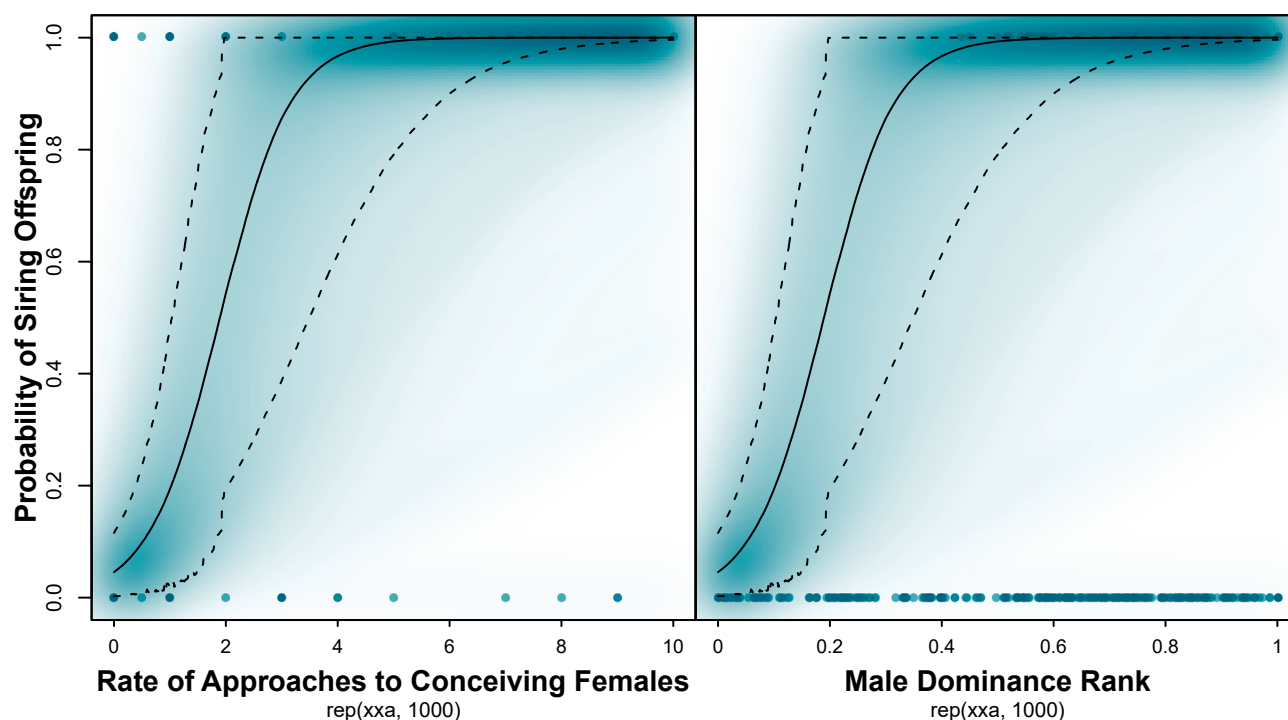


Figure 1. Predictors of paternity success

Model averaged posterior predictions for the effect of the rate of approaches toward conceiving females and male dominance rank on the probability of siring offspring. This plot shows model predictions while holding male rank constant. The solid line represents the mean estimate. The dashed lines represent the 89% highest posterior density interval. The blue cloud shows the full posterior predictions, with darker areas representing higher densities.

toward females shifted closer toward 0 for males of all ranks (Figure 2, Table 2). The model predicted that a male of average rank with no primary associations would approach fully swollen females approximately five times as often as a male of average rank with two or more primary associates (0 primary associates: 1.90 ± 0.85 (median $\pm$ standard error) times per hour; 1 primary associate: 1.23 ± 0.53 times per hour; ≥ 2 primary associates: 0.37 ± 0.21 times per hour). The model also predicts that high-ranking males would approach fully swollen females substantially more often than lower ranking males would, and that males would approach fully swollen females more often when more fully swollen females were present in the group.

Association between involvement in primary associations and paternity success

We were able to examine the relationship between males' involvement in primary associations and paternity success for 45 conceptions involving 25 different females and 11 different sires. The model predicts that high ranking males would sire more infants than lower ranking males would (Table 3). The relationship

Table 1. Effect of rate of approaches to sexually receptive females on paternity success

		Coefficient	Standard Deviation	Lower Bound 95% Credible Interval	Upper Bound 95% Credible Interval	Rhat	Effective Sample Size
Intercept		−2.03	0.45	−2.76	−1.34	1	4649
Main predictor	Rate of approaches	0.47	0.42	−0.18	1.14	1	3877
Fixed Effects	Male dominance rank	1.03	0.39	0.40	1.65	1	5446
	Group Identify (PHG)	−1.45	0.55	−2.34	−0.61	1	3904
Random Effects		1.05	0.30	0.65	1.58	1	567

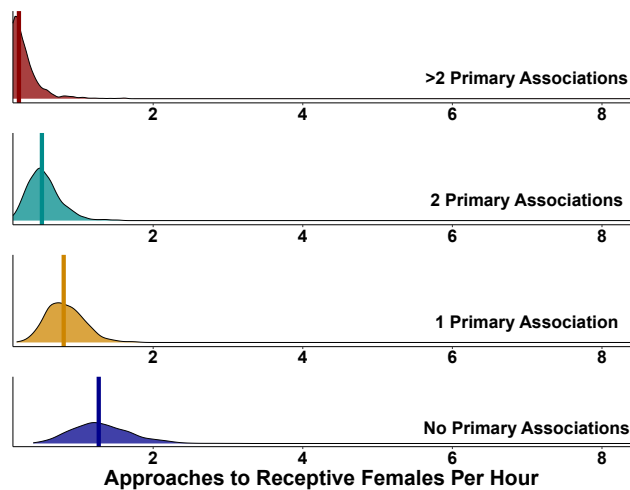


Figure 2. Relationship between number of primary associations and mating effort
Posterior probability distributions from MCMC Bayesian Model of hourly rate of approaches by males of average rank toward fully swollen females. Horizontal panels represent predicted distributions for males with 0, 1, 2, and more than two primary associates. Vertical lines represent median predicted values.

between the number of primary associations that a male was involved in and paternity success was negative, but the credible interval for the coefficient spans 0, indicating that the effect is uncertain (Table 3).

Does participation in primary associations constrain males’ ability to invest in mating effort?

Males are responsible for a smaller proportion of approaches to their primary associates as their number of primary associations on a given day increases (Figure 3, Table 4). The model predicted that males that were involved in one primary association on a given day would initiate $59 \pm 3\%$ of all approaches to their primary associate, males involved in two primary associations would initiate $52 \pm 3\%$ of total approaches, and males involved in more than two primary associations would initiate $45 \pm 4\%$ of all approaches. Note that Figure 3 reflects the full posterior predictive distributions, not arbitrarily specified credible intervals. Although the distributions overlap at their tails, the bulk of their likelihood falls within the peaked sections of the distributions. There was no consistent effect of male rank on the proportion of approaches that males initiated to their primary associates.

DISCUSSION

Our analyses suggest that males make tradeoffs between their investment in mating effort and parenting effort. Males that were involved in more primary associations approached fully swollen females

Table 2. Impact of number of primary associates on rate of approaches to sexually receptive females

		Coefficient (β)	Standard Deviation	Lower Bound 95% Credible Interval	Upper Bound 95% Credible Interval	Rhat	Effective Sample Size
Intercept		0.03	0.43	−0.80	0.87	1	5407
Main predictor	Number of primary associations	−0.46	0.21	−0.91	−0.08	1	5771
Fixed effects	Male Dominance Rank	0.72	0.18	0.37	1.06	1	55831
	Number of sexually receptive females present	0.31	0.07	0.17	0.45	1	6276
	Group Identity (ENK)	0.34	0.37	−0.38	1.05	1	5884
Random intercept effect	Male identity	0.95	0.28	0.52	1.60	1	4067
Random slope effect for number of primary associations	Male identity	0.37	0.26	0.02	0.98	1	2487

Table 3. Impact of the number of primary associates on paternity success

		Coefficient	Standard Deviation	Lower Bound 95% Credible Interval	Upper Bound 95% Credible Interval	Rhat	Effective Sample Size
Intercept		−1.82	0.37	−2.43	−1.26	1	21413
Main predictor	Number of primary associates	−0.26	0.29	−0.73	0.19	1	53137
Fixed Effects	Male dominance rank	1.13	0.31	0.65	1.63	1	5841
	Group Identify (PHG)	−0.89	0.43	−1.58	−0.21	1	4524
Random Effects		0.53	0.21	0.23	0.91	1	324

substantially less often than males that are involved in fewer primary associations, holding the effects of dominance rank constant. Males that were involved in more primary associations were also responsible for initiating a smaller proportion of approaches to their primary associates than males that were involved in fewer primary associations. Differences in the extent of parenting effort did not translate into robust differences in paternity success. Paternity success was negatively related to the number of primary associations that males were involved in, but the credible interval for the coefficient spanned zero, indicating that the effect was somewhat uncertain.

Males' involvement in primary associations seems to limit their involvement in mating effort, which is consistent with the hypothesis that males face tradeoffs between mating effort and parenting effort. The need to trade off mating effort and parenting effort will be influenced by their costs. The costs of males' involvement in primary associations and male parental care are less obvious than the costs of male mating effort. Primary associations do not seem to be energetically demanding or physiologically taxing, and the total amount of time spent interacting with primary associates and infants is relatively small. But primary associations may have hidden costs for males. Male chacma and olive baboons are attentive to the location and safety of their primary associates and their primary associates' offspring.^{31,36} Males that are involved in primary associations have elevated glucocorticoid levels when infanticide risk is high suggesting there are physiological costs to these relationships.²⁵ Although infanticide is more common in chacma baboons than in yellow baboons or olive baboons, it has been documented in all three species.^{57,58} In addition, elevated rates of pregnancy loss and infant death after the immigration of new males that acquire high ranking positions have been documented in yellow baboons.⁵⁹ Thus, males with more primary associates might spend more time scanning for potential threats and maintaining social vigilance than other males, and this may constrain their ability to invest in mating effort. Further research is needed to evaluate the energetic, physiological, and temporal costs of male baboons' involvement in primary associations and male parental care.

Although males' involvement in primary associations had a clear effect on male mating effort, it had less certain negative effects on paternity success. It is possible that we do not have the power to detect an effect of the number of primary associations on paternity success because the sample of conceptions is relatively small, the impact of the rate of approaches to conceiving females on paternity success is relatively weak, and variation in the number of primary associations is compressed within a fairly narrow range. It is also possible that males might behave differently toward conceiving females than other fully swollen females. Males seem to be able to discriminate between conceiving females and other sexually receptive females, because high ranking male yellow baboons preferentially mate guard conceiving females when both conceiving and non-conceiving swollen females are present.²¹ Thus, it is possible that the conception status of females might influence male allocation of investment in mating effort and parenting effort. More data are needed to resolve this question.

We found that males that were involved in more primary associations played a smaller role in establishing proximity to their primary associates than males who were involved in fewer primary associations, and we interpret this as evidence that males operate under temporal constraints. However, we cannot exclude the possibility that females might be more motivated to establish proximity to males that have more primary associates than to males that have fewer primary associates or that there may be variation in the quality of relationships that males have with their primary associates which influences the balance of approaches.

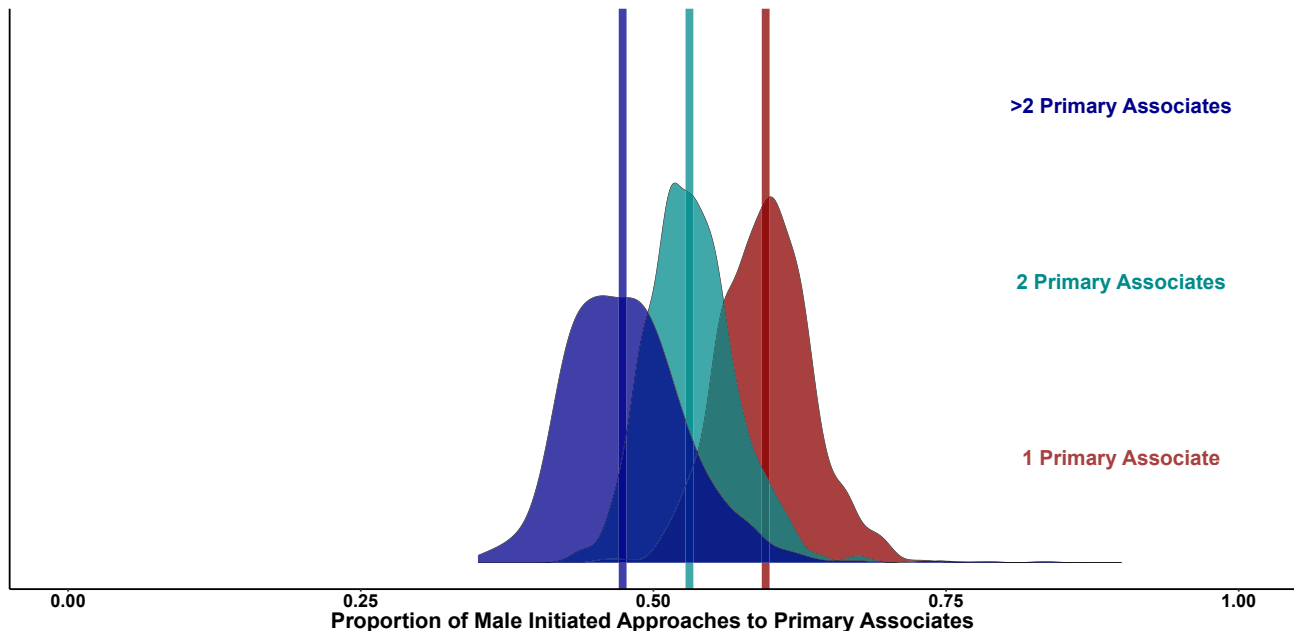


Figure 3. Relationship between number of primary associations and responsibility for initiating proximity

Posterior probability distributions from MCMC Bayesian Model of the proportion of approaches initiated by males toward their primary associates when they have one, two, or more than two primary associates. Vertical lines represent median predicted values.

Previous work indicates that male baboons invest in both mating and parenting effort, and data from the present study suggest that males make tradeoffs between these forms of reproductive effort. Male parenting effort is uncommon in species with polygynandrous mating systems, but an unusual combination of factors may have created conditions that have favored male investment in male parenting effort in single-level baboon societies. These factors include mechanisms that enhance male paternity certainty, relatively high risk of feticide and infanticide, and a prolonged period of development between weaning and sexual maturation.⁶⁰ Further research is needed to understand the conditions that shape the tradeoffs between mating effort and parenting effort in other mammalian taxa with polygynandrous mating systems.

Limitations of the study

This study has several limitations. Most importantly, we cannot quantify the temporal or energetic costs of male investment in mating effort and parenting effort. Such data are difficult to obtain from free ranging animals, but necessary to fully understand the selective forces that shape male reproductive strategies. We also lack evidence that baboon males' participation in primary associations influences the welfare and survival of their offspring. Finally, our analyses are based on data collected over a three-year period on two groups of baboons, and it is not clear whether our findings would extend to other groups, populations, or species of baboons that form single-level societies. Further studies are needed to address these limitations.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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 - Materials availability
 - Data and code availability
- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
 - Subjects
 - Ethical guidelines

Table 4. Factors influencing the proportion of male-initiated approaches to primary associations

		Coefficient (β)	Standard Deviation	Lower Bound 95% Credible Interval	Upper Bound 95% Credible Interval	Rhat	Effective Sample Size
Intercept		−8.53	0.09	−8.72	−8.35	1.00	6291
Main predictor	Number of primary associations	−0.11	0.05	−0.21	−0.01	1.00	5949
Fixed effects	Male Dominance Rank Group	0.02	0.05	−0.08	0.12	1.00	6631
	Identity	−0.19	0.09	−0.36	−0.02	1.00	5994
Random intercept effect	Male identity	0.08	0.07	0.00	0.25	1.00	4862
	Female identity	0.05	0.04	0.00	0.16	1.00	5740
	Dyadic identity	0.06	0.04	0.00	0.17	1.00	5573
Random slope effect	Male identity	0.05	0.04	0.00	0.14	1.00	4606
for number of	Female identity	0.03	0.02	0.00	0.08	1.00	5766
primary associations	Dyadic identity	0.03	0.03	0.00	0.10	1.00	4708

METHOD DETAILS

- Data collection

QUANTIFICATION AND STATISTICAL ANALYSIS

- Male rank determination
- Paternity assessment
- Female reproductive state
- Identification of primary associations
- Data tabulation
- Statistical analyses

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2023.106991>.

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AUTHOR CONTRIBUTIONS

Conceptualization, C.R.H. and J.B.S.; Methodology, C.R.H., S.K.P., and J.B.S.; Formal analysis, C.R.H. and S.K.P.; Data curation, C.R.H. and J.B.S.; Writing—original draft, C.R.H. and J.B.S.; Writing—review and editing, C.R.H., S.K.P., and J.B.S.; Visualization, C.R.H. and S.K.P.; Supervision, J.B.S.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental models: Organisms/strains		
Free-ranging <i>Papio anubis</i> (22 male, 39 female)	Uaso Ngiro Baboon Project, Laikipia, Kenya	N/A
Software and algorithms		
R (4.0.0)		
Brms package (v 2.15.0)		
r-STAN v (Stan Development Team, 2018)		
rethinking' package (v.2.21, McElreath 2016)		
Elo code		22
Other		
Variable measurements and analysis scripts	This paper	Github: https://github.com/crhawley/Tradeoff

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Joan Silk (joansilk@gmail.com).

Materials availability

This study did not generate new unique reagents.

Data and code availability

Data used to conduct the analyses have been deposited on Github and are publicly available as of the date of publication. DOIs are listed in the [key resources table](#).

Code for statistical models has been deposited on Github and is publicly available as of the date of publication. DOIs are listed in the [key resources table](#).

Additional information required to reanalyze the data reported in this paper is available from the [lead contact](#), Joan B. Silk (joansilk@gmail.com) upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Subjects

We studied 22 adult and subadult males and 39 adult and subadult females in two groups of wild olive baboons in the Laikipia region of central Kenya over a 3-year period. The study groups are part of a larger population of baboons that has been monitored by the Uaso Ngiro Baboon Project directed by Dr. Shirley Strum since 1972. The groups that we studied are descendants of Pumphouse Gang (PHG), a group that was translocated from Kekopey (Gilgil), Kenya, to Laikipia in 1984.⁶¹ PHG fissioned in a process that lasted from 2009 to 2011, producing two daughter groups. The larger of the two daughter groups retained the original name, PHG, and the smaller group was named Enkai (ENK). [Table S1](#) shows the number of mature males and mature females in the two study groups over the course of the study period.

The study area is topographically diverse and averages 1718 m above sea level. The habitat is dry savanna and includes grassy plains, acacia woodlands, and dry forests located on the banks of sandy riverbeds. Rainfall is typically concentrated during two wet seasons (March-June, November-December), but droughts have become increasingly common.⁶² An invasive cactus, *Opuntia stricta*, has been spreading through the study area and is now an important component of the baboons' diets.⁶³

Ethical guidelines

This study conformed to U.S. and Kenyan regulations for research. The research was approved by Arizona State University, the National Commission for Science and Technology of Kenya and the Kenya Wildlife Service. All methods for this project were noninvasive and all behavior data was collected on animals well-habituated to human researchers. Observers maintained a distance of 3 meters from study animals at all times. All animal protocols followed the guidelines for the treatment of animals for teaching and research recommended by ASAB/ABS (2014).

METHOD DETAILS

Data collection

We conducted focal observations on all subadult and adult males and females in the two study groups. Females were categorized as subadults when they began experiencing sexual swellings, which typically began when females were about four years of age, and categorized as adults when they produced their first infant, which occurred when they were about 6 years of age. In this population, males begin to develop secondary sexual characteristics and grow larger than adult females when they are about 5-6 years of age. The median age of natal dispersal in this population is 6 years. Males continue to grow, and develop, and reach peak competitive ability when they are 8-10 years of age.³⁵ At the time that the study began, there were six males over the age of 6 years in ENK and 10 in PHG. Several additional males were added to the roster of focal subjects when they were 5-6 years of age, and were included in our analyses. The analyses do not include several males that were not present in the study groups long enough for their ranks to be assessed or for us to collect a sufficient amount of focal data on them. None these males were involved in primary associations with adult females.

Males were observed for approximately 545 hours over a 36-month period. We collected 382.5 hours of observations on 13 males in PHG, and 163.0 hours of observation on 8 males in ENK (three males lived in both groups at some point during the study). All males included in these analyses were present in the study groups for at least 3 months and were observed for at least 3 h (Table S2). The number of observations of each male in each study group varied because not all total males were present for the entire study period or remained in the same group for the entire study group.

During 15-minute focal samples, all approaches to within 1 meter, departures to beyond 1 meter, social interactions, and vocalizations were recorded on a continuous basis. For each of these acts, observers recorded the type of act, the identity of the individual responsible for initiating the act, and the identity of the partner. Behavioral data were collected on hand-held computers, and later transferred to laptop computers for data editing, storage, tabulation, and analysis.

Because the identities of the animals play an important role in the study, the data were not recorded blind. However, the observers were not aware of the specific hypotheses and predictions being tested in this study.

QUANTIFICATION AND STATISTICAL ANALYSIS

Male rank determination

Male rank was determined using Elo-ratings derived from supplants and aggressive dyadic interactions.⁶⁴ The Elo-ratings method uses maximum likelihood fitting of an initial Elo-score when an individual enters the dominance hierarchy, a constant k , and the probability that a focal individual will “win” or “lose” a dominance interaction for each subsequent dominance interaction. Ranks therefore may vary by day, allowing for a male’s prior rank and the results of each dominance interaction to update his rank daily.

Elo calculations were based on approximately 2200 agonistic interactions and supplants that were observed in the two study groups during the 36-month study period. Rankings were scaled so that the highest-ranking male in a group on each day was assigned a rank of 1.00 and the lowest ranking male was assigned a rank of 0.00. Detailed explanation of Elo-rating procedures for this population can be found in ref. 22.

Paternity assessment

We genotyped DNA extracts from non-invasively collected faecal samples of infants, mothers, and potential sires at 13 autosomal microsatellite loci. We then performed parentage analysis in CERVUS 3.0.3⁶⁴ to

assign paternities to infants. In total, sires were assigned to 58 out of 82 offspring (71%) born during the study period. For the remaining offspring, no genotype could be obtained. The putative mother was also genotyped for all these infants and no infant had mismatches with its putative mother at any locus. One mother-offspring-sire trio was assigned with >90% confidence, all others were assigned with >95% confidence. For more details about the parentage analysis, see ref.²²

Female reproductive state

Uaso Ngiri Baboon Project staff regularly monitored female reproductive state. Females were categorized as pregnant, lactating, cycling/flat, cycling/swollen, or cycling/fully swollen on each day of the study. Pregnancy was defined as the period between conception and birth, and the day of conception was computed by counting back 178 days from the date of birth.⁴⁸ Lactation was defined as the period between the day of birth and the date of the first post-partum swelling. Sexual swellings were categorized by size, color, and whether the swelling was inflating or deflating. Females were considered to be fully swollen when they were maximally tumescent and most likely to be in their peri-ovulatory period.⁶⁵ There were some days in which cycling females' reproductive status was not recorded and it was not known whether they had sexual swellings. These are categorized as unknown. On days that males were observed, the reproductive status of 3% of all females was unknown.

Identification of primary associations

Following previous work, focal observations of females were used to identify their primary associates. For each female during each lactation period we tabulated the frequency of her interactions with each of the males in her group. For each individual in each dyad, we calculated the rate of approaches, groom initiations, and grunts as well as the proportion of observation time that each member of the dyad spent grooming and the proportion of time in spent in proximity. These behavioral measures were positively correlated with one another (Table S3). These behavioral measures were used to construct a Dyadic Sociality Index (DSI) which is a composite normalized score assessing the strength of a dyadic relationship.⁵⁶ DSI values were calculated using the following formula:

$$DSI_{xy} = \frac{\sum_{i=1}^d \frac{f_{ixy}}{\bar{f}_i}}{d}$$

To calculate the DSI, the rate of each of behaviors for a given dyad (f_{ixy}) was divided by the mean rate of behavior across all dyads in the two groups ($\bar{f}_i$). Then these values were summed and divided by the number of behaviors in the index (d). The index can vary from 0 to infinity, and higher values represent stronger relationships.

For each female in each lactation period, DSI scores were ranked for all co-resident males. The male with the highest DSI score was considered the primary associate. If the DSI between a female and a second male was within 10% that of the highest DSI value, the second male was also considered a primary associate. Females are assigned the same primary associate(s) for the entire lactation period.

Analyses below are based on primary associations that focal males formed with 26 females across 62 lactation periods. Assessments of females' primary associates during those lactation periods was based on approximately 750 h of focal observations on females. On average females were observed for 13.6 ± 0.7 hr during each lactation period. For 51 lactation periods, mothers were observed from the time that they gave birth until they weaned their infants and resumed cycling when their infants were on average 209.2 ± 9.0 days of age, and in three additional lactation periods mothers were observed from birth until their infants died (at 81, 85, and 191 days of age). Seven lactation periods were ongoing when the study began, and one was ongoing when the study ended.

To confirm that these procedures also reflect male partner preferences,⁶⁶ we also analyzed focal data on males. Analyses of the patterns of approaches initiated by males indicate that males distinguish between the females for whom they have been identified as primary associates and other pregnant and lactating females (Figure S2).

Data tabulation

We calculated the number of male-initiated approaches to resident females on each day that the male was observed. These data were matched with relevant information about the focal male (e.g. current group,

current rank), the reproductive status of his female partners (e.g. reproductive state—pregnant, lactating, cycling/swollen, cycling/flat), and current demographic information (number of females in each reproductive state currently in the group).

For each male, we also tabulated the number of primary associations that he had each day that he was observed. We used the procedures described above to identify primary associations. Primary associations emerge during pregnancy and last through lactation, so primary associations were assumed to begin on the day that the primary associate became pregnant and end on the day when she resumed cycling or the infant died. The number of primary associates that a male had could change from one day to another as the reproductive status of females changed.

We focused our analyses on the number of male-initiated approaches rather than the total time males spent in proximity to females for two reasons. First, proximity is not a directed measure, and does not indicate which party is responsible for initiating proximity. Second, time spent in proximity to fully swollen females was positively correlated with the number of approaches to fully swollen females ($r = 0.46$). A parallel model that assessed the relationship between the number of primary associations and total time in proximity to fully swollen females produced results that were similar to the pattern for the rate of approaches (Figure S3, Table S4).

Statistical analyses

To test whether the rate of approaches to fully swollen conceiving females was a robust predictor of paternity, we modeled the effect of the rate of approaches that males made to fully swollen females during their conception cycles on the probability of becoming the sire of the female's infant. In this model, the outcome variable was paternity (1 = sire, 0 = not sire), and the predictor variables were the rate of approaches (number of approaches per hour), male dominance rank at the time of conception, and group of residence (1 = PHG, 0 = ENK). In this model, male identity was treated as a random intercept variable. We also included random slopes, allowing the effect of the rate of approaches to vary by male and male rank. Continuous predictor variables were standardized to a mean of zero and standard deviation of one. We fitted this model using the `ulam` function in the 'rethinking' package v.2.21,⁶⁷ which uses an efficient Markov chain Monte Carlo, `r-stan` v.2.21.3⁶⁸ to fit Bayesian models in R v.4.1.2.⁶⁹

We used regularizing priors in each of our models, which penalizes overly large effects. Such priors do not allow for undue influence from the prior specification, nor allow for model results to be completely data-driven.⁶⁷ In each of the models, male Elo-scores were standardized so they could be compared across models and meaningfully interpreted.⁶⁷

To test whether males experience a tradeoff between investing in mating effort and parenting effort, we modeled the effect of the number of current primary associations that a male was involved in on a given day on the number of approaches that a male made toward fully swollen females on the same day. In these models, the outcome variable was a count variable: the number of approaches. On 85% of the days when males were observed, no approaches to fully swollen females were observed, and so the outcome variable was zero-inflated (Residual Deviance: Degrees of Freedom, 4833:2006 = 2.41).⁷⁰ Thus, we fit zero-inflated negative binomial (ZINB) generalized linear mixture models (GLMMs) to the data. ZINBs are mixture models that include a logit distribution and a negative binomial distribution. The logit distribution estimates the probability that the number of approaches is zero, while the negative binomial distribution estimates the distribution of approaches of true zeros and counts greater than zero. In these models, positive coefficients from the logit component indicate a higher probability of observing zero instances of behavior (i.e. initiating an approach to a female) while positive values for the negative binomial component indicate more counts of affiliation between a dyad. Each distribution produces a marginal likelihood and the joint likelihood of each behavior is calculated by multiplying the two marginal likelihoods together. These joint likelihoods are then converted to the real scale by using their link functions. For the purposes of real-world predictions, results are presented as number of events per hour.

The main predictor of interest in this model was the number of primary associations a male had on a given day. We controlled for the effects of male dominance rank, the number of fully swollen females in the group on a given day, and group identity. Days in which there were no fully swollen females present (29%, $n = 2835$) were excluded from the analysis. The number of observations per day was included as the offset

term. In this model, male identity was treated as a random intercept variable. We included random slopes, allowing the effect of the number of primary associations to vary by male. For this model, we used the `brm` function in the 'brms' package v 2.15.0 [in R (v 4.0.0)].⁷¹ The brms package is an interface to construct Bayesian models using Hamiltonian MCMC and Stan software.⁶⁸

To assess the effect of the number of primary associates on the proportion of approaches a male made to his primary associates each day, we constructed a binomial GLMM. For each male on each day, we counted the number of times that he approached his primary associates and the number times that his primary associates approached him. Then, we computed the proportion of approaches initiated by the male. The main predictor of interest in this model was the number of primary associations a male had on a given day. We controlled for the effects of male dominance rank and group membership, and we included male identity, female identity, and dyad identity as random intercepts. We included random slopes, allowing the effect of the number of primary associations to vary by male, female, and dyad identity. For this model, we used the `brm` function in the 'brms' package v 2.15.0 in R (v 4.0.0).⁷¹

To test whether male paternity success was influenced by the number of primary associations that a male was current involved in, we constructed a model in which the outcome variable was paternity (1 = sire, 0 = not sire), and the predictor variables were the number of primary associations that a male was involved at the time of conception, male dominance rank at the time of conception, and group of residence (1 = PHG, 0 = ENK). In this model, male identity was treated as a random intercept variable. We also included random slopes, allowing the effect of the rate of approaches to vary by male and male rank. Continuous predictor variables were standardized to a mean of zero and standard deviation of one. We fitted this model using the `ulam` function in the 'rethinking' package v.2.21.⁶⁷

In the tables, we present the magnitude, direction, and standard deviation of variables included in the models. Standard deviations are used to indicate the certainty of an effect, and whether such an effect is reliable and consistent. Because variables change in tandem, individual parameter values do not accurately reflect joint probability effects on posterior probabilities. Thus, we recommend that readers focus on the graphs of posterior distributions which integrate the joint probabilities across multiple variables. Models run in `brms`⁷¹ provide separate estimates for the random slopes and random intercepts, while models run in `Rethinking`⁶⁷ provide composite estimate of the magnitude of the random effect parameters.