

Current Biology

Shifts in Male Reproductive Tactics over the Life Course in a Polygynandrous Mammal

Highlights

- The reproductive tactics of male olive baboons change over the life course
- There is a \cap -shaped relationship between age, dominance rank, and paternity success
- Males often form ties to lactating females whose infants they have sired
- Older males are more likely to form these kinds of ties than younger males are

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In Brief

Silk et al. document age-related shifts in the reproductive tactics of male olive baboons. There is a \cap -shaped relationship between male age, rank, and paternity success, and some males may form ties to the mothers of their infants. Older males are more likely to form these kinds of ties, reflecting changes in payoffs of mating and parenting effort.



Shifts in Male Reproductive Tactics over the Life Course in a Polygynandrous Mammal

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SUMMARY

In polygynous and polygynandrous species, there is often intense male-male competition over access to females, high male reproductive skew, and more male investment in mating effort than parenting effort [1]. However, the benefits derived from mating effort and parenting effort may change over the course of males' lives. In many mammalian species, there is a \cap -shaped relationship between age, condition, and resource holding power as middle-aged males that are in prime physical condition outcompete older males [2–8] and sire more infants [9–12]. Thus, males might derive more benefits from parenting effort than mating effort as they age and their competitive abilities decline [13]. Alternatively, older males may invest more effort in making themselves attractive to females as mates [14]. One way that older males might do so is by developing relationships with females and providing care for their offspring [14, 15]. Savannah baboons provide an excellent opportunity to test these hypotheses. They form stable multi-male, multi-female groups, and males compete for high ranking positions. In yellow and chacma baboons (*Papio cynocephalus* and *P. ursinus*), there is a \cap -shaped relationship between male age and dominance rank [12], and high rank enhances paternity success [12, 16]. Lactating female baboons form close ties (“primary associations” hereafter) with particular males [15–20], who support them and their infants in conflicts [15, 19] and buffer their infants from rough handling [20]. Females' primary associates are often, but not always, the sires of their current infants [16, 20–22].

RESULTS AND DISCUSSION

We examined the effects of male age on reproductive tactics in a 4-year study of wild olive baboons, *P. anubis*, in central Kenya. If

older males derive more benefits from parenting effort than mating effort as they age and their competitive abilities decline, then older males are expected to be more likely to become primary associates of lactating females than younger males are. If older males use primary associations to enhance their future paternity success, then we would expect that being a primary associate would enhance the probability that older males would sire their partners' next infants. Although being a primary associate generally does not enhance future paternity prospects [16, 20, 23], it is possible that this is an effective tactic for the subset of males that are past their physical prime. Finally, if these relationships represent a form of infant care, then primary associates are expected to interact at higher rates with their primary associates' infants than other males do.

There was a clear \cap -shaped relationship between male age and dominance rank (Figure 1; Table S1). Both young and old males held lower ranks than middle-aged males did.

The relationship between male age and dominance rank was reflected in the relationship between male age and paternity success (Figure 2; Table S1). Thus, middle-aged males were more likely to sire infants than younger or older males were.

Males may disperse from one group to another several times during their lives, and it is possible that male dispersal behavior might constrain males' opportunities to become primary associates. However, the sires of 53 of the 55 infants (96%) of known paternity were in the same group as their infants at the time their infants were born, and nearly all of these males remained in their infants' groups throughout the lactation period (89%; $n = 54$ infants observed through lactation), which lasted about 7 months (mean \pm SE: 208.7 \pm 9.3 days).

The probability of becoming a female's primary associate was influenced by both paternity and male age (Figure 3; Table S1). The sires of females' current infants were more likely to become their primary associates than other males were. In addition, the likelihood of becoming a females' primary associate increased with male age. Model comparisons using the Watanabe-Akaike information criterion (WAIC) indicated that the model including age provided a much better fit.

Primary associates were not more likely to sire their partners' next infants than other males were. Our dataset included 30 cases in which the sires of lactating females' next infants were known. In 24 of these cases (80%), females' primary associates



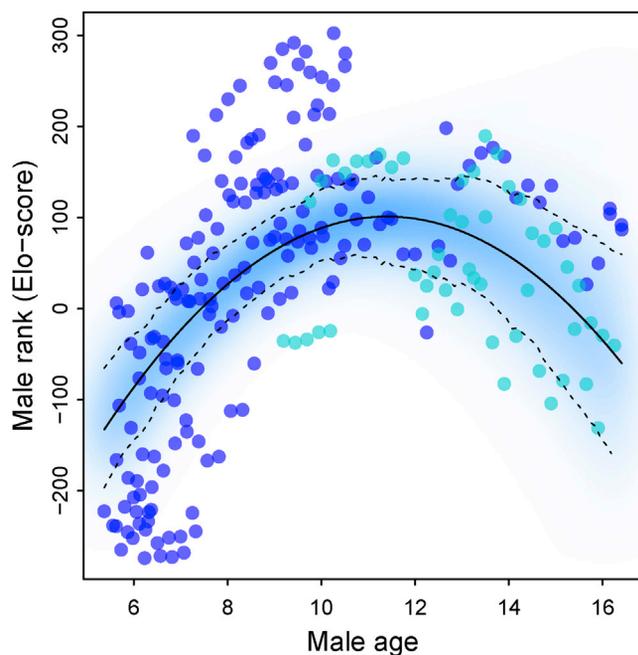


Figure 1. There Is a \cap -Shaped Relationship between Male Age and Dominance Rank

Dark blue indicates that the age for a male was known; light blue indicates that age was estimated. 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. Model sample sizes are as follows: 23 males (4 with estimated ages) and 236 data points. See also Table S1. Figure S1 illustrates the relationship between male age and rank for males of known ages.

were present in their group when they conceived their next infant, but only five became the sires of their partners' next infants. The small number of primary associates that became sires of their partners' next infants means that we have little power to examine the relationship between male age and the probability of siring their partners' next infants systematically. However, the model provides no evidence that being older increased the chance that primary associates would sire their partners' next offspring (Table S2).

Primary associates greeted, inspected, held, and carried their female partners' infants at much higher rates than other males did (Figure 4; Table S3). The model controlling for male age was assigned a substantially higher WAIC weight (0.64) than the model excluding age (0.36). The signs of the coefficients for the male age terms in the model indicate that older males interacted more with infants than younger males did, but the magnitude of the effect of age is small and there is considerable uncertainty around the estimates.

Our data indicate that male olive baboons shift their reproductive tactics as they age and their physical condition declines. Male dominance rank and paternity success have a \cap -shaped relationship with age, male dominance rank, and paternity success, peaking when males are about 9–11 years of age. Both paternity and male age increase the likelihood of becoming a primary associate. Sires are more likely to become primary associates than other males, and as males age, they are

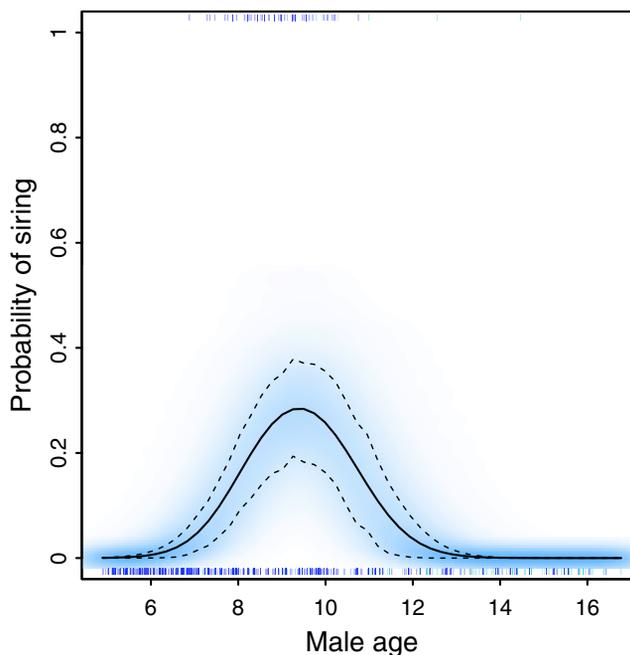


Figure 2. There Is a \cap -Shaped Relationship between Male Age and the Probability of Siring Offspring

Small vertical bars at the top and bottom of the plot show the raw data. Other conventions are as in Figure 1. Model sample sizes are as follows: 26 males (8 with estimated ages), 26 females, 55 infants, and 485 data points. See also Table S1. Figure S2 illustrates the relationship between male age and probability of siring offspring for males of known ages.

progressively more likely to become the primary associates of lactating females. Primary associates were not more likely to become the sires of their partners' next infant than other males, and this pattern did not seem to be influenced by males' age. Primary associates greet, inspect, hold, and carry their partners' infants much more than other males do, suggesting that primary associations are associated with male infant care.

Although males may disperse from one group to another several times during their lives, dispersal did not preclude the possibility of providing extended care for offspring. Sires were nearly always present when their infants were born 6 months after conception, and most remained in their infants' groups through the lactation period, which lasted about 7 months on average. Similarly, in yellow baboon groups, nearly half of all juveniles' fathers remained in their groups until they were at least 3 years of age [24], and the presence of sires enhances offspring growth and development [25]. If male care for offspring influences their fitness, selection might favor males remaining longer in groups in which they have immature offspring. Future research should evaluate whether the presence of immature offspring influences males' dispersal behavior.

The data do not support the hypothesis that becoming a primary associate is an effective mating tactic for older males. However, our ability to detect such an effect was limited because there were relatively few cases in which primary associates sired their partners' next infants and older males sired very few infants overall. Moreover, our analysis was structured to detect differences between categories of males, not the effect of

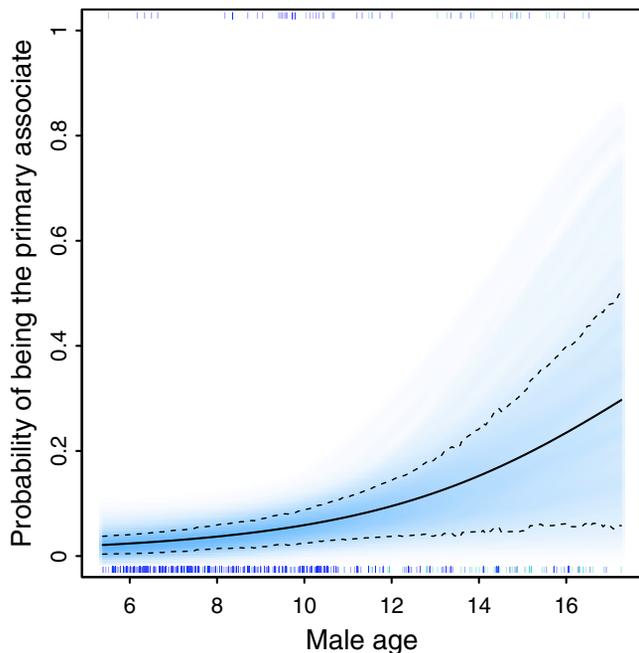


Figure 3. The Probability of Becoming a Primary Associate Increases with Male Age

Small vertical bars at the top and bottom of the plot show the raw data. Other conventions are as in Figure 1. Model sample sizes are as follows: 26 males (8 with estimated ages), 26 females, 55 infants, and 481 data points. See also Table S1. Figure S3 illustrates the relationship between male age and probability of becoming a primary associate for males of known ages.

differences in the behavior of particular males. Thus, it is possible that a male who becomes the primary associate of a particular female is more likely to sire her next infant than if he had not become her primary associate, but this cannot be tested empirically.

Older males were more likely to become primary associates than younger males were when paternity was held constant. This means older males were more likely to become primary associates of both the infants that they had sired and infants that they had not sired. Mismatches between paternity and becoming a primary associate have also been observed in

other baboon populations, but the effects of male age on the likelihood of mismatches has not been investigated before [19–21]. Some researchers have suggested that the mismatch between paternity and becoming a primary associate may arise because males rely on indirect cues of paternity, such as mating activity near the time of conception, and these cues are imprecise [22]. But it is not clear why older males would be more prone to these kinds of errors than younger males. It is possible that males may derive personal benefits from primary associations that shape the development of their relationships with females [20, 26, 27]. Older males may also be influenced by their past paternity history or have a lower threshold for paternity certainty as they age and the relative payoffs from mating effort and parenting effort shift. Further research is needed to resolve this question.

Our cross-sectional analyses indicate that males shift their reproductive tactics as they age, and we would expect this to be reflected in the behavior of individual males over the life course. Our study did not last long enough to track changes in the behavior of individual males over time, but we do not believe this to be a major shortcoming of our analysis. In order for the patterns derived from cross-sectional analyses to be inconsistent with patterns derived from longitudinal analyses, it would be necessary for there to be a link between the probability of forming primary associations and male survival to older ages. More specifically, we would have to posit that there are certain males that form primary associations at high rates when they are in their prime and these males are disproportionately likely to survive to older ages. This does not seem like a likely possibility but should be tested empirically.

An Ω -shaped relationship between age, reproductive effort, and paternity success has been observed in a wide range of taxa, but the kinds of age-related shifts in reproductive tactics that we have documented among olive baboons have not been reported in other taxa. The pattern that we observed among male olive baboons may depend on the existence of a particular constellation of conditions, including (1) the formation of relatively stable mixed-sex groups, (2) males' tolerance of other males in mixed-sex groups, and (3) males' ability to identify their own offspring with some degree of accuracy. These conditions may not be met in many taxa. Stable mixed-sex groups are relatively uncommon in mammals [1]. In species in which males and

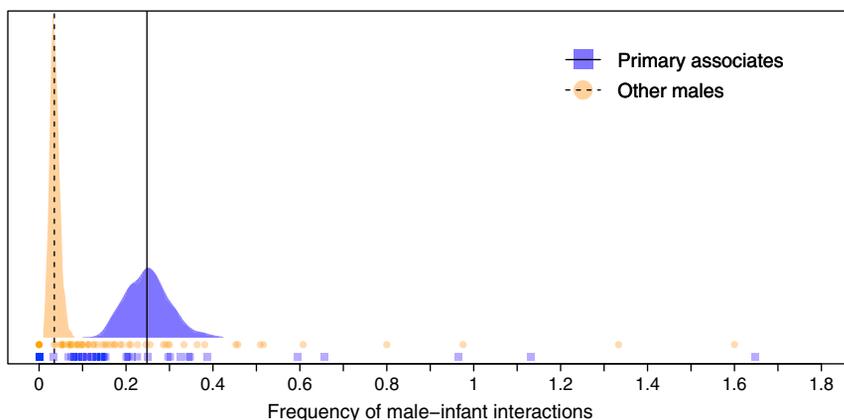


Figure 4. Primary Associates Interact at Higher Rates with Their Partners' Offspring Than Other Males Do

Full posterior predictions for the frequency of interactions between primary associates and infants and between infants and other males. Vertical lines are median posterior predictions. Points show the raw data. The shape of the posterior distributions provides information about the certainty of the estimates. The height of peaks in the posterior distributions indicates the probability of that frequency being observed. Model sample sizes are as follows: 26 males (8 with estimated ages), 26 females, 55 infants, and 485 data points. See also Table S3.

females spend considerable time apart, males have limited opportunities to interact with immatures and may also have reduced male paternity certainty [28].

Stable mixed-sex groups are relatively common among primates [29]. In several species that form multi-male, multi-female groups and have polygynandrous mating systems, males discriminate between their own offspring and the offspring of other males [24, 30–33]. It is possible that males in these species might shift from mating effort to parenting effort as they age and their competitive ability declines. For example, in rhesus macaques, *Macaca mulatta*, there is a \cap -shaped relationship between male age and paternity success [34]. Males interact more with their own infants than they interact with other males' infants, and older males interact with infants at higher rates than younger males do [31]. Thus, rhesus macaques might provide another example of an age-related shift from mating effort to parenting effort. There are also anecdotal reports of older males interacting frequently with immatures in chimpanzees (*Pan troglodytes*) [35], Barbary macaques (*M. arctoides*) [14], and gray langurs (*Semnopithecus entellus*) [14], but it is not clear whether these observations represent a systematic shift in male reproductive tactics with age.

The analyses presented here provide insights about the evolution of male parental care in species without pair bonding, which occurs in some nonhuman primate species, such as baboons and gorillas (*Gorilla gorilla*) [36], and may have characterized our early hominin ancestors [37]. If males are able to identify their offspring with some degree of accuracy based on contextual or phenotypic cues, infants derive benefits from male care, and the relative magnitude of the payoffs derived from mating effort and parenting effort for males vary over the life course, selection may favor temporal shifts in the allocation of mating effort and parenting effort. Factors that increase the value of male care for infants or decrease the benefits derived from intrasexual competition may increase the relative magnitude of the payoffs derived from parenting effort versus mating effort. Understanding the dynamics of these tradeoffs in baboons and other taxa may provide a deeper understanding of the selective pressures that shaped the evolution of the human family.

STAR★METHODS

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

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SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.cub.2020.02.013>.

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AUTHOR CONTRIBUTIONS

E.K.R. was the project field manager and supervised data collection in the field; J.B.S. conceptualized the project, wrote the first draft of the manuscript, and directed the Comparative Analysis of Baboon Sociality project from which the data were drawn; V.S. conducted the genetic analyses of paternity and did the statistical analyses; S.C.S. directed the long-term Uaso Ngiro Baboon Project and provided logistical support for the project; and L.V. supervised the genetic analyses conducted in her lab and provided funding for V.S. All authors reviewed the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental Models: Organisms/Strains		
<i>Papio anubis</i>	Uaso Ngairo Baboon Project, Laikipia, Kenya	N/A
Software and algorithms		
R v.3.5.2.	[38]	PRID: SCR_001905
rethinking 1.59	[39]	Github (https://github.com/rmcclreath/rethinking)
RStan 2.17.3	[40]	Stan (http://mc-stan.org)
Elo_code	[41]	Dryad (https://doi.org/10.5061/dryad.r4g74)
Other		
Variable measurements and analysis scripts	This paper	N/A

LEAD CONTACT AND MATERIALS AVAILABILITY

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Joan B. Silk (joansilk@gmail.com). This study did not generate new unique reagents.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We studied wild olive baboons that range in the Mukogodo region of Laikipia North on the Laikipia Plateau of central Kenya. The groups that we studied are monitored by the Uaso Ngairo Baboon Project directed by Dr. Shirley Strum. For more details about the history of the study population, see [16, 27]

The baboons range in an area that 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. The baboons feed on a variety of grasses, herbs, sedges, and the flowers and the fruits and pods of a variety of shrubs and trees including several *Acacia* species. Recently, *Opuntia stricta*, a non-indigenous cactus, has invaded the area [42], and has become an important part of the diet.

Ethical Guidelines

This research adhered to the legal requirements of Kenyan government, and institutional guidelines at Arizona State University.

METHOD DETAILS

Data Collection Procedures

We collected focal observations on all parous females in the three study groups. During focal samples, observers recorded activity state, social interactions, and vocalizations on a continuous basis. All interactions initiated by the focal female or directed toward the focal female were recorded. In addition, certain interactions (i.e., greeting, inspecting, handling, holding, and carrying) directed toward focal females' infants by others were recorded. For social interactions, observers recorded the type of social behavior, the identity of the partner, and whether the interaction was initiated by the focal animal, the partner, or jointly. For vocalizations, observers recorded the type of call given, the identity of the partner, and whether the call is given by the focal animal or its partner. Observations of aggressive interactions were also collected *ad libitum*.

All data were collected on hand-held computers in the field and later transferred onto computers for error-checking and storage.

Data Tabulation

We defined the "lactation period" for each mother-infant dyad as the time from the day of birth until the resumption of cycling or until the death of the infant if the infant died before the female resumed cycling. The term "current infant" is used to refer to the infant that is currently nursing.

The behavioral data generated information about both instantaneous events (e.g., approaches to within one meter) and states (i.e., proximity within one meter). For each lactation period, we tabulated the number of each type of event for each female-male dyad, and the total duration of time in proximity for each female-male dyad. For events, we divided the number of occurrences by the amount of

time observed when both parties were present in the same social group (co-residence time) to obtain the hourly rate of interaction. For state variables, we divided the total duration of the behavior by the amount of co-residence time to obtain the proportion of observation time.

For the purposes of analyses in this paper, we calculated the rates of approaches to and from lactating females, hourly rates of grunts from males to lactating females, rates of grooming initiations to and from lactating females, the proportion of time lactating females groomed males and were groomed by males, and the proportion of time spent in proximity to males. We also calculated the rate at which males greeted, inspected, held and carried lactating females' infants during focal samples on their mothers.

Identification of Primary Associates

In order to identify females' primary associates, we characterized the strength of the male-female relationships using a composite measure, the dyadic sociality index [43]. The dyadic sociality index (DSI, hereafter), is based on a set of positively correlated behavioral measures (rates of approaches to and from females, hourly rates of grunts from males, rates of grooming initiations to and from females, the proportion of time females groomed males and were groomed by males, and the proportion of time spent in proximity to males). The formula for calculating the DSI is:

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

Where x and y represent a pair of individuals, d is the number of behaviors, f_i is the rate or frequency of behavior i for dyad xy , and \bar{f}_i is the mean rate or frequency of behavior i . Because rates of interactions, and the proportion of time spent in proximity and grooming varied across the study groups, we computed separate means for each group. The DSI can assume values from zero to infinity, with an average value of 1.

For each lactation period, we ranked the DSI score for each of the female's partners. During most lactation periods, the DSI of the top-ranked partner was considerably higher than the DSI of the second-ranked partner, but there a few cases in which the scores for the top two partners were almost identical. For cases in which the DSI of the top-ranked partner was less than 10% larger than the DSI of the second-ranked partner ($n = 7$), we categorized both males as primary associates. For all other cases, only the top-ranked male was categorized as the primary associate. We were unable to identify the primary associate of one female whose infant died shortly after birth.

Assessment of dominance ranks

We used the likelihood-based Elo-rating method [41] to assess male dominance rank over a four-year period. This modeling approach implements maximum likelihood fitting of individuals' initial Elo-scores when entering the hierarchy. The model also fits the constant k which, multiplied by the winning probability of the loser prior to the interaction, determines the increase in Elo-score for the winner and the corresponding decrease in Elo-score for the loser following the interaction. The Elo-rating method generates dominance scores for each individual on each day.

Assessment of paternity

The protocol for the genetic analysis of paternity is described in detail in [16]. In short, we genotyped DNA extracted from non-invasively collected fecal samples of infants, mothers and potential sires at 13 autosomal microsatellite loci. We then performed trio analysis in CERVUS 3.0.3 to assign sires to infants. In total, sires were assigned to 69 infants from our study groups. For all these infants, the mother was also genotyped and no infant had mismatches with its putative mother at any locus. All mother-offspring-sire trios were assigned with > 90% confidence.

Sample Sizes

Analyses of the relationship between male age and male dominance rank were based on 23 different males who resided in the study groups during the study period for at least three months. Analyses of the relationship between male age and paternity were based on a sample of 55 infants who were sired by 11 different males. The number of infants sired by males ranged from 0 to 9. Analyses of the probability of becoming a primary associate and male behavior toward lactating females and their infants during lactation were based on a sample of 55 infants of known paternity. Seventeen different males were involved in primary associations, and the number of primary associations per male ranged from 0-10 over the course of the study period.

QUANTIFICATION AND STATISTICAL ANALYSIS

We fit linear mixed effects models using the `map2stan` function in the 'rethinking' package (v.1.59) [39]. This function uses an efficient Hamiltonian MCMC, `r-STAN` v.2.17.2 [40] to fit models in R v.3.5.2 [38]. In all models, we controlled for the effects of group identity by including group identity as a variable with group ENK as the reference category. We standardized continuous predictors to a mean of zero and a standard deviation of one. We used WAIC statistics for model comparison and performed model averaging according to WAIC weights if one model did not receive all WAIC weight. We compared all models to 'null models' including the intercepts and the

group variable on the basis of WAIC weights. For easier interpretation of the model results, we present mean posterior predictions, 89% highest posterior density intervals (HPDIs) and full posterior distributions (1000 predictions) plotted over the raw data.

We ran a Gaussian linear mixed effects model investigating the relationship between male age and rank. For each male, we extracted the Elo-score at 3-month intervals. We included age as a linear and squared term. In this, and all following models including male age as a predictor, we also included varying intercepts for male identity and varying slopes for male age to control for multiple inclusion of the same males. The results of this model are presented in [Table S1](#), and graphically illustrated in [Figure 1](#).

We fit a binomial linear mixed effects models to assess the influence of age on the probability of siring offspring. In this age model, we included age as a linear and squared term.

We fit a binomial linear mixed effects model to investigate the relationship between male age and a male's probability of being a female's primary associate. We included a categorical variable indicating whether the male partner was the sire of the female's current infant. We accounted for the repeated inclusion of the same individuals and dyads by including varying effects factors. The DSI, which was used to infer primary association, is a dyadic measure derived from behaviors shown by both partners, so specifying a separate varying effect for each individual in the dyad does not accurately pool the information. Instead, we estimated parameters for both individuals simultaneously. In these models each data point represents one mother/infant/male triad. The results of this model are presented in [Table S1](#) and graphically illustrated in [Figure 2](#).

We fit another binomial linear mixed effects model to evaluate whether older males, in contrast to younger males, increased their probability of siring the female's next offspring by being her primary associate. We included an interaction of male age at the estimated time of conception of the next infant and whether a male was the primary associate or not. Male age was included as a linear and squared term. This model was limited to males who were co-resident with the female at the time of the next conception. We compared this model to a model not including the interaction with male age. We also included female identity and the identity of the female-male dyads as varying intercepts. The results of this model are presented in [Table S2](#).

To assess whether primary associates of females interacted with the females' dependent infants more than other males, we constructed a composite index to quantify male-infant relationships. The index was constructed by summing the occurrences of four behaviors each male showed toward an infant (greeting, handling, holding, carrying and inspecting) and dividing this number by the number of hours observed. The distribution of this index was heavily skewed toward zero, so we fitted zero-augmented gamma models with the composite behavioral index as the response variable. Zero-augmented gamma models are mixture models of a Bernoulli distribution, which estimates the probability of the response variable being zero, and a gamma distribution, which estimates the magnitude of the response for values larger than zero. Negative coefficients from the Bernoulli component of the model indicate a lower probability of observing a composite index of zero and higher values for the gamma component indicate higher values of the index when it is larger than zero. The joint likelihood is obtained by multiplying the likelihoods of the Bernoulli and gamma outcomes. We accounted for whether a male was or was not a primary associate. We fitted a second model in which we controlled for male age to allow for potential age effects on the propensity of males to interact with infants. In these models the unit of analysis is the infant/male dyad. The results of this model are presented in [Table S3](#) and graphically illustrated in [Figure 4](#).

We conducted a parallel set of analyses which were restricted to males of known ages. The results of these analyses are very similar to the results based on the full dataset. See [Figures S1](#), [S2](#), and [S3](#) for graphical representations of these model results.

DATA AND CODE AVAILABILITY

The scripts for the statistical models and the datasets necessary to run analyses included in this paper have been deposited in the public depository Git Hub, and are available at: <https://github.com/coryphella/Shifts-in-male-reproductive-tactics>.