



Female age and reproductive stage influence copulation patterns in mountain gorillas' variable mating system

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Abstract

Variation in mating systems and in individuals' copulation patterns can have important consequences for the genetic structure of a population and ultimately its evolution. Whilst most gorilla sub-species form single-male, polygynous reproductive groups, mountain gorillas have both single-male and multimale reproductive groups. Considerable research has investigated the mating patterns of males in these multimale groups, but comparatively little is known about females. We investigated the copulation patterns of 71 female mountain gorillas over 13 years. We found that most sexually active, fecundable females in multimale groups had multiple mating partners. Females' copulation patterns varied based on their reproductive stage, mating most often and with the greatest number of partners when they were pregnant, and least often when they had young dependent offspring. Females copulated throughout pregnancy, with pregnant females copulating more frequently in single-male groups than in multimale groups. Mating also varied with age, with older females mating less often and with fewer partners. Our findings confirm that when females transfer between single-male and multimale groups, they predominantly switch from copulating with one male to copulating with multiple males, and that females are also flexibly adjusting their copulation patterns across their lifetimes. This highlights the considerable variability of the mountain gorillas mating system, particularly from the female perspective, and the importance of accounting for within-species variation in copulation patterns.

Significance statement

Patterns of mating can vary both between individuals of the same species and within individuals across their lives. These patterns influence the genetic structure of a population. By examining copulation patterns in female mountain gorillas, we demonstrate that whilst females in single-male groups have only one mating partner, females in multi-male groups predominantly have multiple partners across a year. They also alter their copulation patterns across their lifetimes, copulating less often and with fewer partners as they age, and copulating most when pregnant. Our results highlight the flexibility with which female mountain gorillas can adjust their copulation patterns across their lifetimes, as the costs and benefits of copulation shift.

Keywords Mating strategy · Ageing · Mating flexibility · Within-species variation · Pregnancy · Conception

Introduction

Animal societies are shaped by the composition of their groups, the relationships within and between these groups and their mating systems (Opie et al. 2012; Kappeler 2019). These elements of the social system can have profound consequences for reproductive skew and the genetic structure of populations (Altmann et al. 1996; Koenig et al. 2013), which ultimately shape a species' evolution. Different elements of the social system are often closely linked, and this is particularly true for group composition and mating system, as in many social species, mating primarily occurs between

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individuals residing in the same group (Clutton-Brock 1989; Kappeler and van Schaik 2002; Prox and Farine 2020).

Mating systems are broadly defined as monogamy, one female mating with one male; polyandry, one female mating with multiple males; polygyny, one male mating with multiple females; and polygynandry, where both males and females have multiple mating partners (Petersdorf and Higham 2018). However, some species do not fall within a single mating system category, and in species with a variable mating system, mating patterns can vary considerably between individuals and even within individuals over time (Davies and Lundberg 1984; Rowell 1988; Lott 1991; Angell et al. 2013; Prox and Farine 2020). For example, cichlid species have been found to vary their mating patterns based on the amount of predation, the sex ratio, the season and male intruder pressure (Lott 1991; Sefc et al. 2009), whilst dunnocks have been found to vary between monogamy, polyandry, polygyny and polygynandry based on the distribution of resources and the ease with which females can be monopolised (Davies and Lundberg 1984).

Phylogenetic analyses suggest that the ancestral mating system of primates was polygynandrous, which subsequently transitioned to polygyny and monogamy in a number of clades (Opie et al. 2012). In group-living primates, mating partners are often limited to those living within the same social group (Kappeler and van Schaik 2002), and evolutionary transitions in group composition and mating strategy have occurred in close succession (Opie et al. 2012). Variable mating systems appear to be relatively scarce in group living primates (Lott 1991; Kappeler and van Schaik 2002). However, our knowledge of such variation is likely limited by data availability and there are a number of notable exceptions, including saddle-back tamarins (Goldizen et al. 1996), black-crested gibbons (Jiang et al. 1999), mountain gorillas (Robbins 1999) and humans (Walker et al. 2011).

Mountain gorillas have a highly flexible social organisation. Whilst reproductive groups in other gorilla subspecies are almost exclusively single-male, composed of a single adult male, one or more females and their offspring (Parnell 2002; Robbins et al. 2004), in mountain gorillas, both single-male and multimale reproductive groups are common (Robbins and Robbins 2018; Hickey et al. 2019). This is because only around half of males and females disperse from their natal group at sexual maturity (Robbins and Robbins 2005; Robbins et al. 2009). Single-male groups are believed to be the ancestral social organisation for mountain gorillas due to the rarity of multimale groups in other gorilla subspecies (Parnell 2002; Robbins et al. 2004), their pronounced sexual dimorphism (Leigh and Shea 1995), their lack of adaptation to sperm competition (Harcourt et al. 1981) and their lack of paternity discrimination (Rosenbaum et al. 2018).

Mating and reproductive skew within multimale mountain gorilla groups from the male perspective has been the focus of considerable research interest (Bradley et al. 2005;

Robbins and Robbins 2005; Stoinski et al. 2009b, c; Robbins et al. 2019). In single-male groups, one adult male benefits from all mating opportunities. In multimale groups, whilst the dominant male usually gains the majority of mating opportunities and paternity, subordinate males also often gain opportunities to mate and sire offspring (Bradley et al. 2005; Nsubuga et al. 2008; Vigilant et al. 2015). However, to understand whether the observed variation in social organisation (single-male and multimale groups) is accompanied with variation in the mating system within these groups, we need an understanding of both male and female mating strategies and copulation patterns.

Extremely little is known about copulation patterns within these multimale groups from the female perspective. Whilst we know males regularly mate with multiple females, copulation patterns have only been reported in detail for 14 females (Robbins 1999). In this study, which examined two multimale groups (one group with two adult males and one with four adult males), 11 out of 14 females were observed copulating with multiple males. Since this study took place, far larger multimale groups have been observed with up to 10 mature males residing in a single group. Females can transfer between groups (both single-male or multimale) multiple times throughout their lives providing an opportunity to alter the identity and number of their mating partners. Females also initiate the majority of copulations (Watts 1991), suggesting that, in addition to the broad-scale mate choices they can make when dispersing between groups, they also have considerable control over finer-scale copulation decisions within their group, involving when, how often and, in the case of multimale groups, with whom they copulate.

Given this level of control, we therefore might expect females to adjust their copulation strategies across their lifetimes as the relative costs and benefits shift. For example, copulating and becoming pregnant at a young age, when female gorillas are still growing themselves (Galbany et al. 2017), could result in a net reduction in reproductive success across the lifetime (Blomquist 2009). In multimale groups, strategic decisions are likely to involve not only the timing and frequency of copulation but also decisions around which partners to copulate with and the total number of partners. Females' reproductive stage is one factor that we would expect to alter the costs and benefits of copulating. For example, during pregnancy, copulations no longer provide a reproductive benefit but may provide alternative benefits in the form of paternity confusion, sexual competition or bond strengthening (Hrdy and Whitten 1987; Doran-Sheehy et al. 2009; Stoinski et al. 2009a; van Noordwijk and van Schaik 2009). When females already have a young infant, the costs of copulation may increase, as having another infant to care for may put the survival of the current infant at risk (Carlisle 1982; Eckardt et al. 2016; Behringer et al. 2022). However, regular suckling

by a current infant, such as that commonly observed by mountain gorillas under 2.5 years, is believed to suppress cycling, reducing the risk of pregnancy (Stewart 1988).

Age is another factor likely to shape reproductive strategies. Reproductive senescence in mid-life (menopause), such as that seen in humans and killer whales is rare (Croft et al. 2017; Johnstone and Cant 2019). Most female mammals reproduce up until death, but many also have rates of reproduction that slow as they age (Packer et al. 1998; Alberts et al. 2013; Lee et al. 2016). These slowing rates of reproduction are likely driven by declines in fertility, such as through the deterioration of ovarian function and higher rates of miscarriage (Harley 1990; Holman and Wood 2001; Robbins et al. 2006). However, there may also be a behavioural component to these reproductive declines, with females copulating less often as they age. Alternatively, females could be copulating more frequently in an attempt to counter the effects of declining fertility. In gorillas, studies of reproductive declines with age have found conflicting results. Robbins et al. (2006) found that in Virunga mountain gorillas, inter-birth intervals of surviving offspring did not increase with the mother's age but did increase with her number of previous births. More recent analyses on the same population have demonstrated that females at the extremes of the age distribution, i.e. the youngest and oldest individuals, had the longest inter-birth intervals (Campos et al. 2022). Examining how the frequency with which female gorillas copulate varies with age will help identify whether these reproductive declines are driven solely by declines in fertility or also by changes in female mating behaviour.

In addition to age-related changes in the frequency with which females copulate, females may also alter their number of partners as they age. Research on social ageing has demonstrated consistent trends across a number of species, including humans and other primates, for older individuals to have fewer social partners (Siracusa et al. 2022). In humans, this increased social selectivity is associated with an emphasis on higher quality, "emotionally close" relationships (Charles and Carstensen 2010). If such age-based social selectivity extends to copulation patterns, we might expect ageing females to have fewer copulation partners even if their overall frequency of copulation remains consistent. Alternatively, a greater number of copulation partners earlier in life could be driven by male preference. Past research has demonstrated that subordinate males may have more opportunities to mate with nulliparous females, as the dominant male may be more tolerant of such copulations, where females may not yet be fertile and there is a high likelihood that the female is their daughter (Watts 1990; Stoinski et al. 2009b). This may enable nulliparous females to copulate with a greater number of partners, whilst the dominant male might prevent parous females from mating with as many partners (Watts 1990).

In this study, we use 13 years of data collected in 9 different multimale gorilla groups to investigate female copulation patterns, testing whether females adjust their frequency of copulations and number of partners with reproductive stage and age. We then examine copulation patterns in detail across pregnancy, comparing copulation frequency across each trimester for females in both multimale and single-male groups. Finally, we examine differences in copulation patterns more broadly between single-male and multimale groups, investigating the variability of the copulation patterns of females that move between single-male and multimale groups. As female mountain gorillas lack outwardly observable signs of cycling or ovulation (Stewart 1988), we primarily refer to copulation patterns (as opposed to mating patterns) throughout, as we cannot determine with certainty whether such copulations could result in reproduction. We refer to mating patterns in a small subset of analyses restricted to only females with a high likelihood of being fecundable given their reproductive stage.

Methods

Study population and data collection

We conducted this study on a subpopulation of Virunga mountain gorillas in the Volcanoes National Park, Rwanda, that has been monitored for over 50 years. These gorillas are habituated to human presence and visited for up to 4 h each day. All gorillas are individually identified based on physical characteristics. Field staff record demographic data, including daily group composition and all births, deaths and transfers between groups. Key behaviours that are observed with lower frequency, including displacements and copulations, are recorded ad libitum (i.e. whenever observed). Data is also recorded using a focal follow approach. A focal individual is chosen semi-randomly (to increase evenness of sampling), and data recorded on them for 50 min. During this focal, any copulations are recorded. Consistent long-term monitoring of this population enabled the age of 88.7% (55 out of 62) of females to be known to an accuracy of within 15 days. Of the remaining 7 females, the ages of 2 were known with an accuracy of ± 1.5 months; 3 females were first observed as subadults, with ages known to an accuracy of ± 1.5 years; and 2 females were first observed as adults. It was not possible to record data blind because our study involved focal animals in the field.

Data extraction

All recorded copulations from both ad libitum and focal data were combined to produce a master dataset of all observed copulations. Whilst focal data is expected to be more complete and some copulations may have been

missed in the ad libitum data, we do not expect any particular bias towards data to be missed from specific individuals within a group. However, it is possible that copulations may be missed more often in larger groups, containing a greater number of sexually active individuals. We therefore accounted for this in our models. In gorillas, copulation often involves specific vocalisations and is therefore less likely to be missed than other behaviour types during group observations (Watts 1991). By combining copulations from both focal ($n=1165$) and ad libitum ($n=3334$) datasets, we could examine a broader picture of copulation patterns within gorilla groups. This is particularly important for the number of copulation partners, on which data would be severely limited if we restricted analyses to focal data alone. As groups were monitored for a maximum of 4 h per day, our data represent a minimum of actual copulation occurrences.

Female copulation data was subdivided into time windows based on each female's reproductive stage and age that were a maximum of 365 days in length. Each female over the age of 6 years in the population was categorised into one of six reproductive stages across the study period: (1) nulliparous, when females had not yet given birth; (2) pregnant, when females were within 260 days prior to giving birth (Robbins 1999; Czekala and Sicotte 2000); (3) infant under 1, when their youngest surviving offspring was under the age of 1 year; (4) infant 1–2, when their youngest surviving offspring was between the age of 1 and 2 years; (5) infant 2 to 3, when their youngest surviving offspring was between 2 and 3 years; (6) no infant under 3, when females were parous but did not currently have an infant under 3 years. Females without offspring under 3 years were combined into a single category, as once a female's offspring reaches 3, she is likely to have begun cycling again (Stewart 1988). If females were pregnant, this category took precedence (e.g. if they had an infant under 3 years but had already become pregnant, they were categorised as pregnant).

Each female's first copulation time window began on the first day of the study (1 January 2003), the date on which the female turned 6 or the first day they were observed in the population over the age of 6 years, whichever was the latest. Each copulation time window ran until the female changed reproductive stage, changed social group, left the study population or until 365 days after the start of the time window, whichever was earlier. If the female remained in the study population, their next copulation time window began on the subsequent day. The age of 6 years onwards, from which we analysed female copulation patterns, is consistent with the age of menarche in female mountain gorillas (Watts 1990).

The number of times a female was observed copulating and their number of partners was extracted for all females in each of their copulation time windows between 2003 and 2015. We also extracted the total number of sexually active

females and males within each female's group during their copulation time window. The observation effort for each female in each time window was calculated based on the number of hours their group was observed within the time period. Copulation time windows of fewer than 60 days or with fewer than 200 observation hours were excluded from all analysis, given the high potential for bias in values based on few days and/or observation hours. Copulation time windows in the remaining sample were a mean (\pm SD) of 285.8 ± 90.8 days in length and based on a mean (\pm SD) of 989.3 ± 398.2 observation hours.

Females were considered to be in multimale groups if more than one adult male (>9 years) was sexually active during their copulation time window. This was cross-referenced against group composition to verify that no other adult males were resident in the group in any cases where only one male was recorded copulating. This enabled us to examine the copulation patterns of 71 females in 9 multimale groups, across 674 time windows, which had the opportunity to copulate with two or more sexually active males.

Frequency of female copulation

The effect of females' reproductive stage and age on their frequency of copulating in multimale groups in each time window was examined using a negative binomial generalised linear mixed model (GLMM). The effect of each reproductive stage was modelled relative to parous females with no offspring under 3 years. The number of sexually active males and number of sexually active females present in the group were also included in the model. The number of hours of observation was accounted for using a log offset term and random effects for individual and group were included. The interaction between reproductive stage and age could not be modelled due to model convergence problems.

Female copulation across male partners

The effect of females' reproductive stage and age on their number of copulation partners in multimale groups in each time window was examined using a GLMM with a Poisson distribution. As previously, the number of sexually active males and females, a log offset term for the number of hours of observation and random effects for individual and group were included. The interaction between reproductive stage and age again could not be modelled due to convergence problems.

To examine variability in mating patterns, i.e. copulation patterns when females were fecundable, we calculated the proportion of fecundable females in multimale groups, monitored over at least 360 continuous days that had 0, 1 and more than 1 mating partner. Fecundable females were defined as those over the age of 9 years (mean age of first birth = 9.99 years (Morrison et al. 2022)) that were not

pregnant and did not have an infant under 3 years (mean surviving inter-birth interval = 4.09 years (Morrison et al. 2022)). This included 8 nulliparous and 41 parous time windows across 27 females.

Conception and pregnancy

All female copulation data across periods when females were pregnant in either single-male ($n=24$ pregnancies in 15 females) or multimale groups ($n=95$ pregnancies in 47 females) were examined. Each pregnancy was split into three trimesters, defined as T1: 260–174 days prior to birth; T2: 173–88 days prior to birth; and T3: 87–1 day prior to birth (Robbins 1999; Czekala and Sicotte 2000). Copulation patterns were only examined for trimesters in which the female's group was observed for at least 100 h ($N=350$ trimesters from 119 pregnancies of 51 females). We examined changes in copulation frequency across pregnancy and between group types using a negative binomial GLMM, including group type (single-male or multimale), trimester, and the interaction between group type and trimester as predictor variables. A random effect for the specific pregnancy, nested within female ID, was included, along with a log offset term for the number of hours of observation.

We examined the number of partners across each trimester for females in multimale groups using a GLMM with a Poisson distribution, including trimester as a predictor, a random effect for the pregnancy nested within female ID and a log offset term for observation hours. We also examined the number of copulation partners for females in multimale groups in the period surrounding conception in more detail. We extracted their monthly number of copulation partners and hours of observation in the 5 months surrounding the date of conception (i.e. the month of conception and the 2 months either side). The month of conception was estimated as the 15 days either side of the estimated date of conception, 260 days prior to birth (Robbins 1999; Czekala and Sicotte 2000). The influence of month relative to conception on the number of partners was modelled using a GLMM with a Poisson distribution, with a log offset term to account for observation hours. Pregnancy but not female ID was included as a random effect, due to issues of model convergence.

Variability in copulation patterns across group types

We compared the frequency of copulations in single-male and multimale groups using a negative binomial GLMM ($N=674$ female time windows, from 71 females in 16 groups). Group type was included as a predictor, with female ID and group included as random effects, and a log offset

term for the number of hours of observation. We then identified the proportion of females that had resided in both types of groups across the study period, examining whether any of these females copulated exclusively with a single partner when residing in a multimale group.

Model fitting and checking

All models were fitted by maximum likelihood using the 'lme4' R package. Models were checked for overdispersion and zero inflation using the 'performance' R package, and where identified, an alternative distribution (e.g. negative binomial) was used and models rechecked to ensure overdispersion or zero inflation were no longer present. All models were compared against null models which contained all control and random effect variables but no predictor variables, by ANOVA using AIC.

Results

Frequency of female copulation

The frequency with which females in multimale groups were observed copulating was strongly influenced by their age and reproductive stage (Table 1, Fig. 1). Pregnant females copulated most frequently, significantly more often than parous females without an infant under 3 (the reference category). This was followed by nulliparous females, whose frequency of copulating did not differ significantly from parous females without an infant under 3. Females with infants under the age of 1 year mated least frequently, with 88.6% of females in this reproductive category never observed copulating, 8.0% observed copulating once and 3.4% observed copulating twice ($n=88$ time windows). Females with infants under the age of 2 also rarely copulated, with 78.6% never observed copulating, 15.7% observed copulating once and 5.7% observed copulating multiple times ($n=70$). The majority of females appear to start becoming sexually active again when their offspring is between 2 and 3 years old. Copulations by females in this reproductive stage are still less frequent than in females without an infant under 3 (Table 1), but 54.3% of females with offspring between 2 and 3 years old were observed copulating at least once ($n=70$).

The frequency of copulation also declined with the age of the female (Table 1). As females effectively do not copulate when their infant is under 2 years and appear to copulate at high frequencies during pregnancy regardless of age (Fig. 1), this pattern appears to be driven primarily by females that do not have infants under the age of 2 years. Frequency of copulation was not influenced by either the number of sexually active males or females present in the group.

Table 1 The effect of reproductive stage, age, number of sexually active males and number of sexually active females, on the frequency with which females copulated. The effect of reproductive stage was relative to parous females with no infant under the age of 3 years. Effects were modelled using a generalised linear mixed model with a negative binomial distribution, random effects for individual and group and a log offset term for the number of hours the female's group was observed. Number of observations = 546, from 71 females in 9 groups

Number of copulations (negative binomial GLMM)				
Comparison of full and null model: $X^2=413.69$, $p<0.001$				
	Est	Std. error	Z	Pr(> z)
(Intercept)	-1.656	0.291	-5.690	<0.001
Nulliparous	0.164	0.207	0.790	0.430
Pregnant	0.496	0.153	3.249	0.001
Infant under 1 year	-4.190	0.329	-12.745	<0.001
Infant aged 1–2 years	-3.276	0.268	-12.238	<0.001
Infant aged 2–3 years	-1.404	0.200	-7.025	<0.001
Age	-0.210	0.094	-2.241	0.025
No. of sexually active males	0.021	0.029	0.722	0.470
No. of sexually active females	-0.011	0.022	-0.524	0.600

Female copulation across male partners

Nulliparous females, pregnant females and parous females with no infants under the age of 3 (the reference category) had the greatest number of copulation partners in multimale groups (Table 2, Fig. 1). Females with infants in the under 1-, 1–2- and 2–3-year categories had the fewest partners, with a significant reduction in partners compared to parous females without an infant under 3 years (Table 2, Fig. 1). Females were observed copulating with more partners, the greater the number of sexually active males in the group, but observed copulating with fewer partners, the greater the number of sexually active females in the group (Table 2). The number of partners a female had declined strongly with age. Again, this appeared to be driven by females that did not have infants under the age of 2 years and were not pregnant, as females with infants under 2 rarely copulated, regardless of age, and pregnant females copulated with a high number of partners, regardless of age (Fig. 1).

Mating patterns were examined in fecundable females monitored for at least 360 continuous days. This included 8 nulliparous and 41 parous female time windows across 27 individuals. All nulliparous females mated with more than one male across the year they were observed. Ten parous females did not mate (24.4%), 9 mated with only one partner (22.0%) and 22 mated with multiple partners (53.7%). Overall, of the 39 fecundable female years in which a female was

sexually active, 76.9% involved mating with multiple males, whilst 23.1% involved mating with only one male.

Conception and pregnancy

Females in both multimale ($n=95$ pregnancies in 47 females) and single-male groups ($n=24$ pregnancies from 15 females) consistently copulated across pregnancy (Fig. 2A), and females in multimale groups consistently copulated with multiple partners across pregnancy (Fig. 2B). Females in single-male groups copulated more frequently during pregnancy than those in multimale groups (Table 3), and this difference was greatest in the first trimester (Fig. 2A). Although trimester did not predict the frequency of copulation overall, the effect of trimester on the frequency of copulation differed between single-male and multimale groups (Table 3), with frequencies declining in single-male groups as the pregnancy progressed but remaining relatively stable across the pregnancy in multimale groups (Fig. 2A). In multimale groups, females' number of copulation partners did not differ across trimesters ($X^2 = 2.832$, $df = 2$, $p=0.243$; Fig. 2B). Number of partners also did not differ across the months leading up to and immediately following conception ($X^2 = 2.876$, $df = 4$ $p=0.579$; Fig. 3).

Variability in copulation patterns across group types

We compared the frequency of copulations in single-male and multimale groups (674 time windows, from 71 females in 16 groups). Females in single-male groups did not mate more often than those in multimale groups overall ($n=674$, $est=-0.280 \pm 0.251$, $z=-1.116$, $p=0.265$). Almost half of the females studied (47.9%, 34 out of 71) had resided in both single-male and multimale groups across the 13-year study period, and 26 were observed copulating in both group types. All but one of the 26 females observed copulating in both group types mated with more than one partner in at least one time window. These females copulated with multiple males in 72 of the 128 time windows (56.3%) in which they resided in a multimale group and were observed copulating. The one female that was observed copulating with only one male at a time had three time windows in a multimale group in which she was observed copulating. In one of these, she was only observed copulating once, and in another, she was only observed copulating twice, suggesting that this perceived single-male strategy may be the result of too few copulation observations. However, in the final period, she was observed copulating 28 times with a single male (the dominant male), despite the presence of two other sexually active males in the group. None of the males were known kin; however, the two males with which she did not copulate were more than 15 years younger than her compared to the male she did copulate with who was 9.8 years younger than her.

Discussion

Our findings support past research (Robbins 1999) demonstrating that mating in multimale mountain gorilla groups is predominantly polygynandrous, with most fecundable and sexually active females copulating with multiple partners in a year. We confirm that females predominantly change from copulating with only one male, to copulating with multiple males when they transfer between single-male and multimale groups. This variability in mating system is a trait shared with humans, one of gorillas' closest evolutionary relatives, who show even greater flexibility with monogamy, polygyny, polyandry and polygynandry all observed (Walker et al. 2011; Schacht and Kramer 2019). In other African apes, less variation in group composition is observed and mating strategy closely resembles group composition, i.e. with polygynandry in multi-male, multi-female chimpanzee and bonobo groups and polygyny in single-male, multi-female western gorilla groups (Parnell 2002; Robbins et al. 2004; Petersdorf and Higham 2018; Moscovice et al. 2019).

Copulation patterns within multimale mountain gorilla groups are strongly affected by females' reproductive stage. Females rarely copulate when they have offspring under the age of 2 years, and copulate less frequently when they have offspring aged between 2 and 3 years, compared to those without young offspring. This gradual resumption of copulating coincides with weaning, as infants reduce their frequency of suckling from around 2.5 years (Stewart 1988) and reach nutritional independence around 3.3 years (Eckardt et al. 2016). This weaning likely enables a transfer of investment from current to future offspring, with associated hormonal changes resulting in a resumption of cycling and an increase in mating behaviours (Stewart 1988; Habumuremyi et al. 2014).

Contrary to previous studies in this population (Watts 1990, 1991; Robbins 1999), our large sample has enabled us to demonstrate that some females are copulating when they still have young unweaned offspring. However, this still represents a minority of females, most of whom were observed copulating only once over a period of up to a year. Further hormonal analyses are required to determine the point at which females commonly resume cycling following a birth, and the extent to which pregnancy is prevented by lactation inhibiting cycling (lactational amenorrhea), by residual lactational infertility (infertility after cycling has resumed) or by the extremely low rates of copulation. For example, in capuchin monkeys, lactation prevents cycling for roughly 5 months following birth, during which copulations do not occur. This is followed by a further 10 months of residual lactational infertility during which females are cycling and copulating, but do not become pregnant (Recabarren et al. 2000). Both lactational amenorrhea and residual lactational infertility are common across primates, including humans

(Diaz et al. 1995), baboons (Altmann et al. 1978), macaques (Aso et al. 1985) and colobus monkeys (Harris and Monfort 2006). In gorillas, the absence (or extremely low rates) of copulation by females with young infants is likely to provide redundancy with lactation-based mechanisms, increasing the reliability with which pregnancy is prevented. It is also highly likely that these mechanisms are interlinked, with hormonal changes simultaneously leading to lower proceptivity in females and inhibiting cycling or fertility (Ziegler et al. 2000; Habumuremyi et al. 2014; Calik-Ksepka et al. 2022).

Nulliparous females did not copulate more frequently or with more partners than parous females without infants under 3. However, as nulliparous females represent almost all females under the age of 8 years (Fig. 1), it is not possible to disentangle the effect of being very young, from being nulliparous. Older females copulated less frequently and with fewer partners than younger females. The decline in frequency of mating with age suggests that age-based declines in reproduction in this species (Robbins et al. 2006; Campos et al. 2022) are, in part, behaviourally driven. Hormonal analyses have suggested that ovarian function may decline as mountain gorillas age, with geriatric females cycling less frequently (Habumuremyi et al. 2016). The combination of lower rates of copulation and declining ovarian function is likely to limit reproduction later in life. At this point, it may be more advantageous for females to invest in current offspring than future offspring, given older mothers' low rates of offspring survival (Campos et al. 2022) and increased risk of dying before offspring are weaned (Robbins et al. 2006). It is also possible that age-related hormonal changes may directly drive the reduction in copulations if rates of cycling decline with age, as copulations are more frequent in the days surrounding ovulation (Habumuremyi et al. 2014, 2016). Further research on copulation patterns across the lifespan in other species will help elucidate the extent to which behavioural changes are responsible for age-related changes in female reproduction more broadly, as well as the potential for hormonal changes to drive these behavioural changes.

The decline in number of copulation partners with age suggests that females are not just mating less frequently but are also becoming more selective in their choice of partner, mirroring age-based changes observed in social behaviour in other species (Siracusa et al. 2022). Inbreeding avoidance and male preference also represent potential explanations for the decline in female copulation partners with age. Female relatedness to male group members would be expected to increase with group tenure, as their male offspring reach maturity (Ellis et al. 2022), which may effectively reduce their number of options for copulation partners later in life if they remain in the same social group. Dominant males may also be more tolerant of other males copulating with young

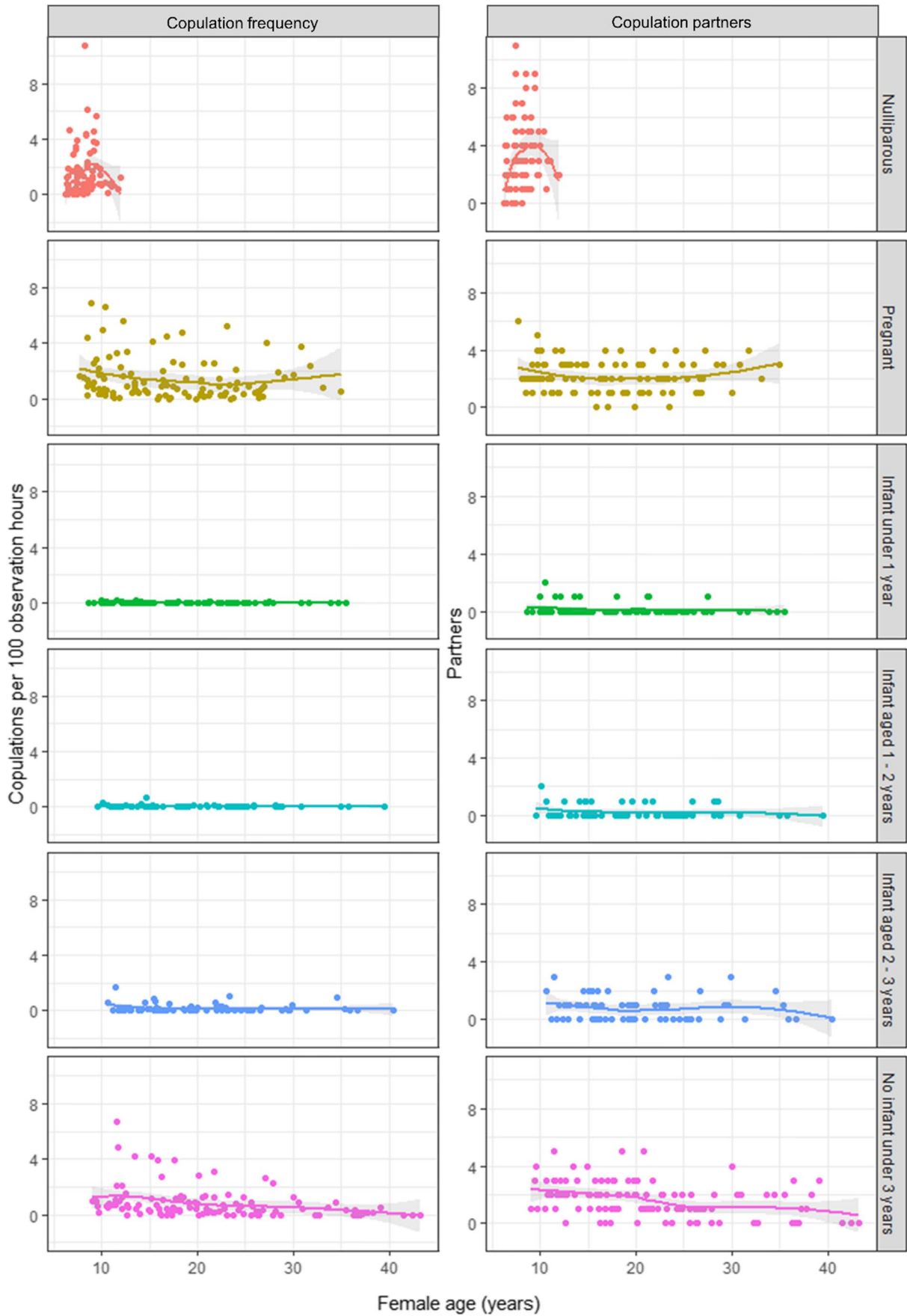


Fig. 1 Females' frequency of copulation and number of partners during each reproductive period, across age. Dots indicate values during each reproductive stage across a maximum of 1 year. Lines indicate smoothed averages across age for each reproductive stage, calculated using the loess function. Grey shading indicates 95% confidence intervals

females that could be their daughters (Watts 1990; Stoinski et al. 2009b). Finally, males may be less receptive to older females if they are less fertile or at greater risk of dying prior to weaning of offspring (Robbins et al. 2006; Campos et al. 2022). However, a major caveat to these analyses is that due to sampling most females over only a small proportion of their reproductive life, we were unable to directly demonstrate these age-based changes within individuals, taking a broader comparative approach across individuals.

The frequency with which females in multimale groups copulated did not change based on the number of sexually active males or females in their group. This contrasts with previous research demonstrating that females copulate more on days when they are the only receptive female compared with days when multiple females are receptive (Watts 1990). This difference, however, is likely to be driven by the time scales over which these behaviours were examined and suggests that whilst female competition may limit access to males and thus copulation frequency over a single day, it does not hinder access to the same extent over the longer periods of up to a year that we examine. A female's number of copulation partners increased with the number of sexually active males present, suggesting that females choose to increase their number of partners given a greater number of options. Number of partners also decreased with the number of sexually active females present. In combination with the lack of effect on copulation frequency, these findings suggest that females are ultimately able to copulate at their desired frequency but may face competition over access to certain partners and the timing of those copulations. However, all analyses related to the number of sexually active group members and particularly those predicting copulation frequency must be interpreted with caution, due to the possibility that a greater number of copulations were missed during ad libitum sampling in larger groups.

Copulating with multiple males around the time of conception is a common strategy for infanticide avoidance, but a potential cost is that females reduce their capacity to choose which male they reproduce with (Smuts 1987). Mountain gorillas have high male reproductive skew, with the dominant male siring the majority of offspring (Nsubuga et al. 2008; Vigilant et al. 2015). This could occur through dominant males gaining more copulation opportunities or by females copulating with them more often when they are most fertile. Females could reduce their number of partners when most fertile to increase the

likelihood of a high-quality male siring their offspring. This would enable some level of female choice regarding the paternity of their offspring whilst still allowing them to gain the benefits associated with copulating with multiple males. However, we found no evidence that females in multimale groups were reducing their number of partners in the month of conception, relative to the months on either side. This suggests that if females are reducing their number of partners during their most fertile periods, this is occurring over time scales shorter than a month.

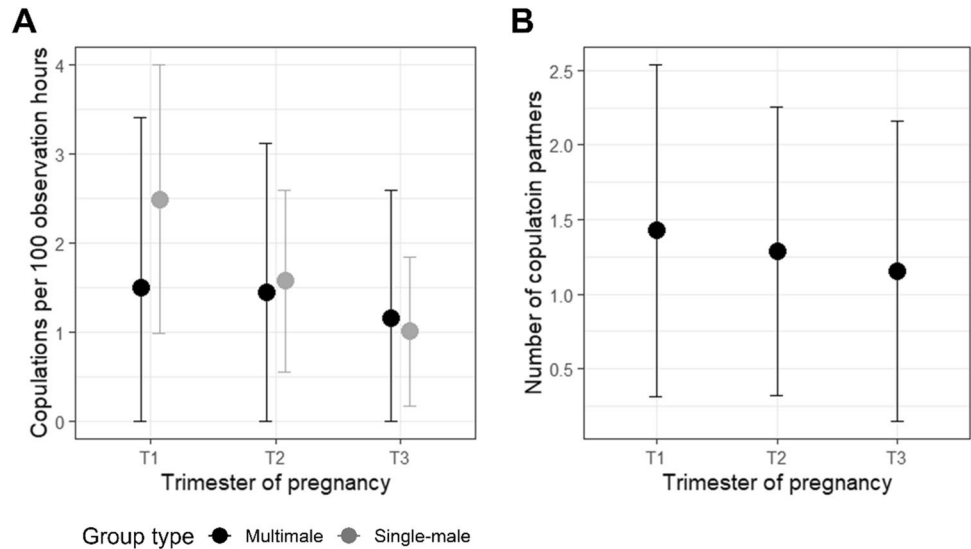
One of the most unusual aspects of female gorilla's copulation patterns is the frequency with which they copulate during pregnancy. We found that females consistently copulated throughout pregnancy, and that this occurred at the highest frequency of all female's reproductive stages. In multimale groups, this occurred with a consistent number of male partners across the trimesters. Post-conception copulations in multimale groups are commonly explained as a paternity confusion strategy, such that multiple males could feasibly have fathered the offspring and therefore may provide paternal care, or be less likely to commit infanticide (van Noordwijk and van Schaik 2009). However, post-conception copulations also occur in primates in single-male groups due to the additional benefits they can confer, such as increased protection or feeding opportunities for the female, or through sexual competition with other females via sperm depletion (van Noordwijk and van Schaik 2009).

Such post-conception copulations occur in single-male western lowland gorilla groups, where females are more

Table 2 The effect of reproductive stage, age, number of sexually active males and number of sexually active females, on female's number of copulation partners. The effect of reproductive stage was modelled relative to parous females with no infant under the age of 3 years. Effects were modelled using a generalised linear mixed model with a Poisson distribution, random effects for individual and group and a log offset term for the number of hours the female's group was observed. Number of observations = 546, from 71 females in 9 groups

Number of copulation partners (Poisson)				
Comparison of full and null model: $X^2=483.96$, $p<0.001$				
	Est	Std. error	Z	Pr(> z)
(Intercept)	-3.054	0.153	-19.925	<0.001
Nulliparous	-0.031	0.139	-0.220	0.826
Pregnant	0.144	0.108	1.341	0.180
Infant under 1 year	-2.977	0.311	-9.564	<0.001
Infant aged 1–2 years	-2.419	0.263	-9.201	<0.001
Infant aged 2–3 years	-0.997	0.159	-6.282	<0.001
Age	-0.210	0.059	-3.578	<0.001
No. of sexually active males	0.057	0.017	3.386	0.001
No. of sexually active females	-0.044	0.014	-3.056	0.002

Fig. 2 Copulation patterns across pregnancy for females in multimale and single-male groups. **A** The frequency of copulations observed across each trimester in multimale and single-male groups. **B** A female's number of partners across each trimester in multimale groups. Points indicate means and error bars indicate the standard deviation



likely to copulate on days when other females are sexually active (Doran-Sheehy et al. 2009; Stoinski et al. 2009a). We found post-conception copulations were common in both single-male and multimale mountain gorilla groups but occurred at higher frequency in single-male groups, particularly during the first trimester. This could be driven by sexual competition between females in single-male groups, where females have greater potential to monopolise copulations limiting the capacity of other females to reproduce (Doran-Sheehy et al. 2009; Stoinski et al. 2009a). Sexual competition, particularly close to the time of conception, may also provide greater benefits in single-male groups where only one adult male is available to protect young offspring from infanticide by outgroup males (Robbins et al. 2013). This higher frequency of female copulation in single-male groups

relative to multimale groups during pregnancy was not found more broadly across reproductive stages, suggesting this is not merely driven by more efficient sampling in single-male groups.

The lack of change in frequency of copulation across the trimesters in pregnant females in multimale groups and the lower frequency of copulation overall relative to pregnant females in single-male groups suggests that paternity confusion is not a major driver of copulation patterns during pregnancy. This contrasts with patterns seen in many other primate species (van Noordwijk and van Schaik 2009) but is unsurprising given the rarity of infanticide by males from within the same group, and the lack of paternity discrimination in male care (Watts 1989; Rosenbaum et al. 2015, 2018). Females in other primate species have often been

Table 3 The effect of trimester of pregnancy (T1–3) and group type (multimale vs single-male) on copulation frequency. Effects were modelled using a generalised linear mixed model with a negative binomial distribution. A random effect for the pregnancy, nested

within female ID was included, and a log offset term for the number of hours the group was monitored whilst the female was in each trimester of pregnancy. $N=350$ trimesters from 119 pregnancies of 51 females.

Comparison of full and null model: $\chi^2=26.719$, $p<0.001$

	Est	Std. error	Z	Pr(> z)	χ^2	p
(Intercept)	−1.486	0.141	−10.572	<0.001		
Trimester of pregnancy (relative to T1)					3.432	0.064
T2	0.003	0.107	0.029	0.977		
T3	−0.207	0.112	−1.855	0.064		
Group type (single-male)	0.768	0.257	2.983	0.003	13.297	0.001
Stage of pregnancy:group type interactions (relative to T1:multimale)					9.708	0.008
Q2:single-male	−0.463	0.217	−2.133	0.033		
Q3:single-male	−0.702	0.234	−2.999	0.003		

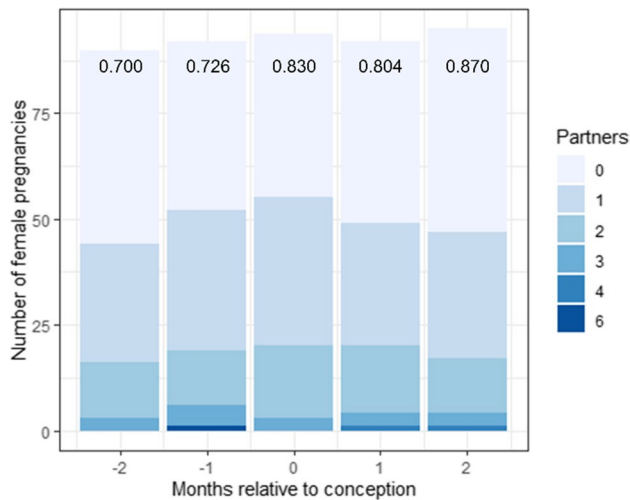


Fig. 3 Females' number of observed copulation partners in each month of the 5 months surrounding conception. Month of conception estimated as the 15 days either side of the estimated date of conception (260 days prior to birth). Mean number of copulation partners per month provided at the top of each bar

documented copulating outside of fertile periods in response to encountering unfamiliar males, e.g. following a group takeover (Hrdy and Whitten 1987; Sommer et al. 1992), but such events are again, extremely rare in mountain gorillas.

So why are post-conception copulations so widespread across gorilla group types? Sexual competition provides one adaptive explanation, although one with reduced strength in multimale groups. An alternative is that post-conception copulations could help establish and maintain strong social relationships, which benefit the offspring through enhanced protection or access to resources (Hrdy and Whitten 1987; Nguyen et al. 2009; van Noordwijk and van Schaik 2009). This may help explain why we found that copulations were most frequent during pregnancy compared to all other reproductive stages, as a close relationship with a male could be particularly valuable when females are about to have a young infant. Finally, it has also been theorised that copulations during pregnancy could merely be an artifact of hormonal changes during pregnancy (Hrdy and Whitten 1987).

Overall, our findings demonstrate that multimale mountain gorilla groups have a highly variable mating system, such that, as females flexibly transfer between groups of differing composition, they are switching between polygynous and polygynandrous mating. Females also flexibly adjust their copulation patterns based on their age, reproductive stage and group composition. We show that although copulations are extremely rare when females have dependent infants, they can still occur. Females also copulate throughout pregnancy,

and this occurs most frequently in single-male groups during the first trimester—indicating the role of sexual competition in shaping these copulation patterns. Older females copulate less often and with fewer partners, suggesting a behavioural component to female gorillas' decline in reproduction with age. This research highlights the flexibility with which female mountain gorillas can adjust their copulation patterns across their lifetimes, adding to our fairly limited understanding of variable mating systems within non-human primates. Such research can further our understanding of how flexible copulation patterns such as our own may have evolved, and the selective pressures that have shaped evolutionary transitions between social organisations and mating systems.

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Author contributions The study was conceived by REM with further development by all authors. Data was collected and curated by Dian Fossey Gorilla Fund field staff and researchers including EN and WE, and managed by TSS, EN and WE. Data was extracted by EN and REM. Analyses were run by REM. The first draft of the manuscript was written by REM and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability All data analysed during this study are included in this published article and its supplementary information files.

Declarations

Ethics approval Research relied on non-invasive behavioural observations of wild mountain gorillas which was approved by the Rwanda Development Board and conducted in accordance with the ethical standards of the Dian Fossey Gorilla Fund and the International Primate Society's Code of Best Practices for Field Primatology.

Conflict of interest The authors declare no competing interests.

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References

- Alberts SC, Altmann J, Brockman DK, Cords M, Fedigan LM, Pusey A, Stoinski TS, Strier KB, Morris WF, Bronikowski AM (2013) Reproductive aging patterns in primates reveal that humans are distinct. *P Natl Acad Sci USA* 110:13440–13445. <https://doi.org/10.1073/pnas.1311857110>
- Altmann J, Altmann SA, Hausfater G (1978) Primate infant's effects on mother's future reproduction. *Science* 201:1028–1030. <https://doi.org/10.1126/science.98844>
- Altmann J, Alberts SC, Haines SA et al (1996) Behavior predicts genetic structure in a wild primate group. *P Natl Acad Sci USA* 93:5797–5801. <https://doi.org/10.1073/pnas.93.12.5797>
- Angell RL, Butlin RK, Altringham JD (2013) Sexual segregation and flexible mating patterns in temperate bats. *PLoS One* 8:e54194. <https://doi.org/10.1371/journal.pone.0054194>
- Aso T, Williams RF, Aso T (1985) Lactational amenorrhea in monkeys: effects of suckling on prolactin secretion. *Endocrinology* 117:1727–1734. <https://doi.org/10.1210/endo-117-5-1727>
- Behringer V, Berghänel A, Deschner T, Lee SM, Fruth B, Hohmann G (2022) Transition to siblinghood causes a substantial and long-lasting increase in urinary cortisol levels in wild bonobos. *eLife* 11:e77227. <https://doi.org/10.7554/eLife.77227>
- Blomquist GE (2009) Trade-off between age of first reproduction and survival in a female primate. *Biol Lett* 5:339–342. <https://doi.org/10.1098/rsbl.2009.0009>
- Bradley BJ, Robbins MM, Williamson EA, Steklis HD, Steklis NG, Eckhardt N, Boesch C, Vigilant L (2005) Mountain gorilla tug-of-war: silverbacks have limited control over reproduction in multimale groups. *P Natl Acad Sci USA* 102:9418–9423. <https://doi.org/10.1073/pnas.0502019102>
- Calik-Ksepka A, Stradczusk M, Czarnecka K, Grymowicz M, Smolarczyk R (2022) Lactational amenorrhea: neuroendocrine pathways controlling fertility and bone turnover. *Int J Mol Sci* 23:1633
- Campos FA, Altmann J, Cords M et al (2022) Female reproductive aging in seven primate species: patterns and consequences. *P Natl Acad Sci USA* 119:1–10. <https://doi.org/10.1073/pnas.2117669119>
- Carlisle TR (1982) Brood success in variable environments: implications for parental care allocation. *Anim Behav* 30:824–836. [https://doi.org/10.1016/S0003-3472\(82\)80156-5](https://doi.org/10.1016/S0003-3472(82)80156-5)
- Charles ST, Carstensen LL (2010) Social and emotional aging. *Annu Rev Psychol* 61:383–409. <https://doi.org/10.1146/annurev.psych.093008.100448>
- Clutton-Brock TH (1989) Mammalian mating systems. *Proc R Soc Lond B* 236:339–372. <https://doi.org/10.1098/rspb.1989.0027>
- Croft DP, Johnstone RA, Ellis S, Nattrass S, Franks DW, Brent LJN, Mazzi S, Balcomb K, Ford JKB, Cant MA (2017) Reproductive conflict and the evolution of menopause in killer whales. *Curr Biol* 27:298–304. <https://doi.org/10.1016/j.cub.2016.12.015>
- Czekala N, Sicotte P (2000) Reproductive monitoring of free-ranging female mountain gorillas by urinary hormone analysis. *Am J Primatol* 51:209–215. [https://doi.org/10.1002/1098-2345\(200007\)51:3<209::AID-AJP6>3.0.CO;2-6](https://doi.org/10.1002/1098-2345(200007)51:3<209::AID-AJP6>3.0.CO;2-6)
- Davies NB, Lundberg A (1984) Food distribution and a variable mating system in the dunnoek, *Prunella modularis*. *J Anim Ecol* 53:895–912. <https://doi.org/10.2307/4666>
- Diaz S, Seron-Ferre M, Croxatto HB, Veldhuis J (1995) Neuroendocrine mechanisms of lactational infertility in women. *Biol Res* 28:155–163
- Doran-Sheehy DM, Fernández D, Borries C (2009) The strategic use of sex in wild female western gorillas. *Am J Primatol* 71:1011–1020. <https://doi.org/10.1002/ajp.20743>
- Eckardt W, Fawcett K, Fletcher AW (2016) Weaned age variation in the Virunga mountain gorillas (*Gorilla beringei beringei*): influential factors. *Behav Ecol Sociobiol* 70:493–507. <https://doi.org/10.1007/s00265-016-2066-6>
- Ellis S, Johnstone RA, Cant MA et al (2022) Patterns and consequences of age-linked change in local relatedness in animal societies. *Nat Ecol Evol* 6:1766–1776. <https://doi.org/10.1038/s41559-022-01872-2>
- Galbany J, Abavandimwe D, Vakiener M, Eckardt W, Mudakikwa A, Ndagijimana F, Stoinski TS, McFarlin SC (2017) Body growth and life history in wild mountain gorillas (*Gorilla beringei beringei*) from Volcanoes National Park, Rwanda. *Am J Phys Anthropol* 163:570–590. <https://doi.org/10.1002/ajpa.23232>
- Goldizen AW, Mendelson J, Van Vlaardingen M, Terborgh J (1996) Saddle-back tamarin (*Saguinus fuscicollis*) reproductive strategies: evidence from a thirteen-year study of a marked population. *Am J Primatol* 38:57–83. [https://doi.org/10.1002/\(SICI\)1098-2345\(1996\)38:1<57::AID-AJP6>3.0.CO;2-S](https://doi.org/10.1002/(SICI)1098-2345(1996)38:1<57::AID-AJP6>3.0.CO;2-S)
- Habumuremyi S, Robbins MM, Fawcett KA, Deschner T (2014) Monitoring ovarian cycle activity via progestagens in urine and feces of female mountain gorillas: a comparison of EIA and LC-MS measurements. *Am J Primatol* 76:180–191. <https://doi.org/10.1002/ajp.22220>
- Habumuremyi S, Stephens C, Fawcett KA, Deschner D, Robbins MM (2016) Endocrine assessment of ovarian cycle activity in wild female mountain gorillas (*Gorilla beringei beringei*). *Physiol Behav* 157:185–195. <https://doi.org/10.1016/j.physbeh.2016.02.017>
- Harcourt AH, Harvey PH, Larson SG, Short RV (1981) Testis weight, body weight and breeding system in primates. *Nature* 293:55–57. <https://doi.org/10.1038/293055a0>
- Harley D (1990) Aging and reproductive performance in langur monkeys (*Presbytis entellus*). *Am J Phys Anthropol* 83:253–261. <https://doi.org/10.1002/ajpa.1330830213>
- Harris TR, Monfort SL (2006) Mating behavior and endocrine profiles of wild black and white colobus monkeys (*Colobus guereza*): toward an understanding of their life history and mating system. *Am J Primatol* 68:383–396. <https://doi.org/10.1002/ajp.20232>
- Hickey JR, Granjon AC, Vigilant L et al (2019) Virunga 2015–2016 surveys: monitoring mountain gorillas, other select mammals, and illegal activities. GVTC, IGCP & partners, Kigali, Rwanda
- Holman DJ, Wood JW (2001) Pregnancy loss and fecundability in women. In: Ellison PT (ed) *Reproductive Ecology and Human Evolution*. Transaction Publishers, New Brunswick, NJ, USA, pp 15–38
- Hrdy SB, Whitten PL (1987) Patterning of sexual activity. In: Smuts B, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) *Primate Societies*. University of Chicago Press, Chicago, pp 370–384
- Jiang X, Wang Y, Wang Q (1999) Coexistence of monogamy and polygyny in black-crested gibbon (*Hylobates concolor*). *Primates* 40:607–611. <https://doi.org/10.1007/BF02574835>
- Johnstone RA, Cant MA (2019) Evolution of menopause. *Curr Biol* 29:R112–R115
- Kappeler PM (2019) A framework for studying social complexity. *Behav Ecol Sociobiol* 73:13
- Kappeler PM, van Schaik CP (2002) Evolution of primate social systems. *Int J Primatol* 23:707–740
- Koenig A, Scarry CJ, Wheeler BC, Borries C (2013) Variation in grouping patterns, mating systems and social structure: what

- socio-ecological models attempt to explain. *Phil Trans R Soc B* 368:20120348. <https://doi.org/10.1098/rstb.2012.0348>
- Lee PC, Fishlock V, Webber CE, Moss CJ (2016) The reproductive advantages of a long life: longevity and senescence in wild female African elephants. *Behav Ecol Sociobiol* 70:337–345. <https://doi.org/10.1007/s00265-015-2051-5>
- Leigh SR, Shea BT (1995) Ontogeny and the evolution of adult body size dimorphism in apes. *Am J Primatol* 36:37–60. <https://doi.org/10.1002/ajp.1350360104>
- Lott D (1991) Intraspecific variation in the social systems of wild vertebrates. Cambridge University Press, Cambridge
- Morrison RE, Hirwa JP, Ndagijimana F, Vecellio V, Eckardt W, Stoinski TS (2022) Cascading effects of social dynamics on the reproduction, survival, and population growth of mountain gorillas. *Anim Conserv* (published online). <https://doi.org/10.1111/acv.12830>
- Moscovice LR, Surbeck M, Fruth B et al (2019) The cooperative sex: sexual interactions among female bonobos are linked to increases in oxytocin, proximity and coalitions. *Horm Behav* 116:104581. <https://doi.org/10.1016/j.yhbeh.2019.104581>
- Nguyen N, Van Horn RC, Alberts SC, Altmann J (2009) Friendships between new mothers and adult males: adaptive benefits and determinants in wild baboons (*Papio cynocephalus*). *Behav Ecol Sociobiol* 63:1331–1344. <https://doi.org/10.1007/s00265-009-0786-6>
- Nsubuga AM, Robbins MM, Boesch C, Vigilant L (2008) Patterns of paternity and group fission in wild multimale mountain gorilla groups. *Am J Phys Anthropol* 135:263–274. <https://doi.org/10.1002/ajpa.20740>
- Opie C, Atkinson QD, Shultz S (2012) The evolutionary history of primate mating systems. *Commun Integr Biol* 5:458–461. <https://doi.org/10.4161/cib.20821>
- Packer C, Tatar M, Collins A (1998) Reproductive cessation in female mammals. *Nature* 392:807–811. <https://doi.org/10.1038/33910>
- Parnell RJ (2002) Group size and structure in western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. *Am J Primatol* 56:193–206. <https://doi.org/10.1002/ajp.1074>
- Petersdorf M, Higham JP (2018) Mating systems (primates). In: Trevaathan W (ed) *The International Encyclopedia of Biological Anthropology*. Wiley, Hoboken, NJ, pp 1–5
- Prox L, Farine D (2020) A framework for conceptualizing dimensions of social organization in mammals. *Ecol Evol* 10:791–807. <https://doi.org/10.1002/ece3.5936>
- Recabarren MP, Vergara M, Martínez MC, Gordon K, Serón-Ferré M (2000) Impact of lactation upon fertility in the New World primate capuchin monkey (*Cebus apella*). *J Med Primatol* 29:350–360. <https://doi.org/10.1034/j.1600-0684.2000.290507.x>
- Robbins MM (1999) Male mating patterns in wild multimale mountain gorilla groups. *Anim Behav* 57:1013–1020. <https://doi.org/10.1006/anbe.1998.1063>
- Robbins AM, Robbins MM (2005) Fitness consequences of dispersal decisions for male mountain gorillas (*Gorilla beringei beringei*). *Behav Ecol Sociobiol* 58:295–309. <https://doi.org/10.1007/s00265-005-0917-7>
- Robbins MM, Robbins AM (2018) Variation in the social organization of gorillas: life history and socioecological perspectives. *Evol Anthropol* 27:218–233
- Robbins MM, Bermejo M, Cipolletta C, Magliocca F, Parnell RJ, Stokes E (2004) Social structure and life-history patterns in western gorillas (*Gorilla gorilla gorilla*). *Am J Primatol* 64:145–159. <https://doi.org/10.1002/ajp.20069>
- Robbins AM, Robbins MM, Gerald-Steklis N, Steklis HD (2006) Age-related patterns of reproductive success among female mountain gorillas. *Am J Phys Anthropol* 131:511–521. <https://doi.org/10.1002/ajpa.20474>
- Robbins AM, Stoinski TS, Fawcett KA, Robbins MM (2009) Leave or conceive: natal dispersal and philopatry of female mountain gorillas in the Virunga volcano region. *Anim Behav* 77:831–838. <https://doi.org/10.1016/j.anbehav.2008.12.005>
- Robbins AM, Gray M, Basabose A, Uwingeli P, Mburanumwe I, Kagoda E, Robbins MM (2013) Impact of male infanticide on the social structure of mountain gorillas. *PLoS One* 8:e78256. <https://doi.org/10.1371/journal.pone.0078256>
- Robbins MM, Akantorana M, Arinaitwe J et al (2019) Dispersal and reproductive careers of male mountain gorillas in Bwindi Impenetrable National Park, Uganda. *Primates* 60:133–142. <https://doi.org/10.1007/s10329-019-00718-z>
- Rosenbaum S, Hirwa JP, Silk JB, Vigilant L, Stoinski TS (2015) Male rank, not paternity, predicts male-immature relationships in mountain gorillas, *Gorilla beringei beringei*. *Anim Behav* 104:13–24. <https://doi.org/10.1016/j.anbehav.2015.02.025>
- Rosenbaum S, Vigilant L, Kuzawa CW, Stoinski TS (2018) Caring for infants is associated with increased reproductive success for male mountain gorillas. *Sci Rep* 8:15223. <https://doi.org/10.1038/s41598-018-33380-4>
- Rowell TE (1988) Beyond the one-male group. *Behaviour* 104:189–201. <https://doi.org/10.1163/156853988X00511>
- Schacht R, Kramer KL (2019) Are we monogamous? A review of the evolution of pair-bonding in humans and its contemporary variation cross-culturally. *Front Ecol Evol* 7:230
- Sefc KM, Hermann CM, Koblmüller S (2009) Mating system variability in a mouthbrooding cichlid fish from a tropical lake. *Mol Ecol* 18:3508–3517. <https://doi.org/10.1111/j.1365-294X.2009.04295.x>
- Siracusa ER, Higham JP, Snyder-Mackler N, LJM B (2022) Social ageing: exploring the drivers of late-life changes in social behaviour in mammals. *Biol Lett* 18:20210643
- Smuts BB (1987) Sexual competition and mate choice. In: Smuts B, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) *Primate Societies*. University of Chicago Press, Chicago, pp 385–399
- Sommer V, Srivastava A, Borries C (1992) Cycles, sexuality, and conception in free-ranging langurs (*Presbytis entellus*). *Am J Primatol* 28:1–27. <https://doi.org/10.1002/ajp.1350280102>
- Stewart KJ (1988) Suckling and lactational anoestrus in wild gorillas (*Gorilla gorilla*). *J Reprod Fertil* 83:627–634. <https://doi.org/10.1530/jrf.0.0830627>
- Stoinski TS, Perdue BM, Legg AM (2009a) Sexual behavior in female western lowland gorillas (*Gorilla gorilla gorilla*): evidence for sexual competition. *Am J Primatol* 71:587–593. <https://doi.org/10.1002/ajp.20692>
- Stoinski TS, Rosenbaum S, Ngaboyamahina T, Vecellio V, Ndagijimana F, Fawcett K (2009b) Patterns of male reproductive behaviour in multi-male groups of mountain gorillas: Examining theories of reproductive skew. *Behaviour* 146:1193–1215. <https://doi.org/10.1163/156853909X419992>
- Stoinski TS, Vecellio V, Ngaboyamahina T, Ndagijimana F, Rosenbaum S, Fawcett KA (2009c) Proximate factors influencing dispersal decisions in male mountain gorillas, *Gorilla beringei beringei*. *Anim Behav* 5:1155–1164. <https://doi.org/10.1016/j.anbehav.2008.12.030>

- van Noordwijk MA, van Schaik CP (2009) Reproductive patterns in eutherian mammals: adaptations against infanticide? In: van Schaik CP, Janson CH (eds) *Infanticide by Males and its Implications*. Cambridge University Press, Cambridge, U. K., pp 322–360
- Vigilant L, Roy J, Bradley BJ, Stoneking CJ, Robbins MM, Stoiniski TS (2015) Reproductive competition and inbreeding avoidance in a primate species with habitual female dispersal. *Behav Ecol Sociobiol* 69:1163–1172. <https://doi.org/10.1007/s00265-015-1930-0>
- Walker RS, Hill KR, Flinn MV, Ellsworth RM (2011) Evolutionary history of hunter-gatherer marriage practices. *PLoS One* 6:e19066. <https://doi.org/10.1371/journal.pone.0019066>
- Watts DP (1989) Infanticide in mountain gorillas: new cases and a reconsideration of the evidence. *Ethology* 81(1-8):18. <https://doi.org/10.1111/j.1439-0310.1989.tb00754.x>
- Watts DP (1990) Mountain gorilla life histories, reproductive competition, and sociosexual behavior and some implications for captive husbandry. *Zoo Biol* 9:185–200. <https://doi.org/10.1002/zoo.1430090302>
- Watts DP (1991) Mountain gorilla reproduction and sexual behavior. *Am J Primatol* 24:211–225. <https://doi.org/10.1002/ajp.1350240307>
- Ziegler T, Hodges K, Winkler P, Heistermann M (2000) Hormonal correlates of reproductive seasonality in wild female Hanuman langurs (*Presbytis entellus*). *Am J Primatol* 51:119–134. [https://doi.org/10.1002/\(SICI\)1098-2345\(200006\)51:2<119::AID-AJP2>3.0.CO;2-O](https://doi.org/10.1002/(SICI)1098-2345(200006)51:2<119::AID-AJP2>3.0.CO;2-O)

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