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Mothers may shape the variations in social organization among gorillas

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When mothers continue to support their offspring beyond infancy, they can influence the fitness of those offspring, the strength of social relationships within their groups, and the life-history traits of their species. Using up to 30 years of demographic data from 58 groups of gorillas in two study sites, this study extends such findings by showing that mothers may also contribute to differences in social organization between closely related species. Female mountain gorillas remained with their sons for significantly longer than western gorillas, which may explain why male philopatry and multimale groups are more common among mountain gorillas. The presence of the putative father and other familiar males did not vary significantly between species, and we found only limited support for the socio-ecological theory that the distribution of adult males is influenced by the distribution of females. Within each gorilla species, variations in those distributions may also reflect the different stages in the typical life cycle of a group. Collectively, our results highlight the potentially far-reaching consequences of maternal support that extends beyond infancy,

1. Introduction

One of the primary goals of behavioural ecology has been to understand the distributions of adult males and females, including the proportion of breeding groups that are one-male versus multimale [1–3]. Socio-ecological theories predict that the number of adult males per group is mainly determined by the spatio-temporal distribution of sexually receptive females, and the number of adult females per group is influenced by predation risks and the distribution of food resources [4–7]. The number of adult females per group may also be influenced by the number of adult males, particularly if the risk of infanticide is lower in multimale groups than in one-male groups [8,9]. The distributions of adult males and females are shaped by the relative costs and benefits of dispersal versus philopatry [10,11].

The costs and benefits of dispersal (relative to philopatry) may depend on support from parents and other relatives that extends beyond infancy [12,13]. For example, a mother may assist her son in agonistic interactions with other group members, and enhance his access to potential mates, which can influence subsequent male dispersal patterns [14–16]. Maternal support of daughters may facilitate the nepotistic female dominance relationships of many cercopithecines, as well as the post-reproductive lifespan of humans [17–19]. Despite imperfect kin discrimination mechanisms, fathers can support their offspring in agonistic interactions, and provide protection against infanticide and predators [20,21]. Maturing male siblings may emigrate together to maintain coalition partners and reduce the costs of dispersal [22,23]. Dispersal can reduce inbreeding and increase inclusive fitness by reducing competition among kin [24–26]. Life-history parameters can affect the probability that individuals will reach adulthood with their parents and other relatives, but further study is needed to more fully understand the implications for differences in dispersal patterns and social organization among species [27,28].

This paper examines the variations in social organization between/within populations of mountain gorillas (*Gorilla beringei beringei*) and western lowland gorillas (*Gorilla gorilla gorilla*), including the potential influence of parents and other relatives. Gorillas are interesting species for studies of social organization because they represent an important model for understanding the evolution of human behaviour [29–32]. Gorillas are also interesting because both sexes may disperse or remain philopatric, thereby playing a direct role in shaping their group compositions [33–35]. Natal and secondary dispersal are both common for females, who transfer directly to a solitary male or to another group [35–37]. By contrast, adult males (silverbacks) typically become solitary when they emigrate, and they rarely immigrate into breeding groups [34,38,39]. A one-male group is formed when females transfer to a solitary male, and it can become an (age-graded) multimale group when their male offspring reach adulthood [2,40]. A multimale group may become one-male if it fissions, if a subordinate silverback emigrates, or if a silverback dies. When the dominant silverback dies in a multimale breeding group of mountain gorillas, a subordinate silverback inherits the group, and the immature males remain in the group [40,41]. When the dominant silverback dies in a one-male group, the group typically disintegrates, and its immature males may join non-breeding groups [35,42]. If a high proportion of males reach adulthood in non-breeding groups, then the proportion of breeding groups that contain multiple adult males may be correspondingly low.

Approximately 40% of mountain gorilla groups are multimale, versus only 5% for western gorillas, so socio-ecological theories predict that mountain gorilla groups will contain more adult females [43,44]. The largest groups are typically found with mountain gorillas (as expected), but the median group size has not differed significantly among gorilla species [45]. The socio-ecological predictions may be weakened for gorillas because silverbacks rarely immigrate into breeding groups, which limits the potential for the distribution of males to adjust to changes in the distribution of females [38,40].

Less than half of male mountain gorillas disperse upon reaching adulthood, which is significantly lower than the nearly universal dispersal of male western gorillas [38,39]. Those results are consistent with the higher proportion of multimale groups among mountain gorillas, because male philopatry is the primary mechanism for breeding groups to become multimale [40]. Studies of male mountain gorillas have provided only limited support for socio-ecological expectations, however, because the probability of dispersal has not been consistently correlated with the number of adult females or the adult sex ratio in the group [38,40] (but see [46]). Instead, the probability of dispersal was significantly lower if the mother of the potential emigrant was still in the group [38]. Philopatric males had significantly higher

copulation rates than males who ultimately emigrated, which suggested that staying in close proximity to their mother could give males more access to other adult females [38]. If the presence of the mother can influence the dispersal patterns and social organization of mountain gorillas, then does it also account for the differences between mountain gorillas versus western gorillas?

In addition to facilitating relationships with other adult females, the mother could help her sons to develop a stronger relationship with the dominant silverback [38]. Those relationships may also be stronger if the sons are with a 'familiar' dominant silverback such as their putative father, especially if such familiarity is used as proxy for kin discrimination [47,48]. Silverbacks are considered 'familiar' if they were in the group when the potential emigrant was an infant (even if they were not silverbacks at the time). In other words, the potential emigrant grew up with the familiar males, who may include his brothers, half-brothers and his putative father. We define the putative father as the silverback who was dominant when the potential emigrant was first observed as an infant. Dominant silverback mountain gorillas were in close proximity with philopatric subordinates more frequently than with the males who subsequently emigrated, so tolerant relationships could increase the probability for groups to remain multimale [38]. Further study is needed to compare the probabilities for males in each gorilla species to reach adulthood with a dominant silverback who is their putative father or another familiar male.

To examine whether mothers may influence the variations in social organization among mountain gorillas and western gorillas, we compared the probabilities for males in each species to reach adulthood in the same group as their mother. If mothers account for the higher proportion of male philopatry and multimale groups among mountain gorillas, then we expect male western gorillas to have a significantly lower probability of reaching adulthood with their mother. We performed similar comparisons of the probabilities for males to reach adulthood with a dominant silverback who is their putative father or another familiar male. To examine the potential consequences when the dominant silverback dies, we compared the probability for males in each species to reach adulthood in a breeding group (versus a non-breeding group or solitary). To re-examine the socio-ecological theories that the distribution of males is influenced by the distribution of females, we compared the average number of adult females in breeding groups of mountain gorillas versus western gorillas, as well as the average number of adult females in one-male versus multimale groups within each population. Based on the socio-ecological theories, we would expect mountain gorilla groups to contain more adult females than western gorillas, and we expect multimale groups to contain more adult females than one-male groups. We discuss these results within the context of the socio-ecological theories and other potential explanations for the variations in social organization among gorillas and other species, including the development of male philopatry among Homininae.

2. Material and methods

Demographic data for mountain gorillas were obtained from the long-term records of the International Gorilla Conservation Programme, the Rwanda Development Board, the Institut Congolais pour la Conservation de la Nature, and the Uganda Wildlife Authority. Mountain gorillas were monitored in 19 groups throughout the Virunga volcano region from June 1979 to April 2010 [41,49]. Data for western gorillas were obtained from the long-term records at Mbeli Bai, a swampy forest clearing in the Nouabalé-Ndoki National Park, Republic of Congo [35,50–52]. Western gorillas were monitored in 39 groups from February 1995 to December 2014. See electronic supplementary material, §S1 for more details about the study sites.

We used a mixed effect Cox model [53] to compare the probabilities for male mountain gorillas and western gorillas to reach adulthood in the same group as their mother. The analysis used a separate data point for each immature male who was observed since infancy (106 mountain gorillas and 96 western gorillas). The predictor variable was the gorilla species. The random effect variables were the identity of the mother and the group where the male was first observed. The response variable was the 'normalized' age of the immature males, which we defined as their actual age divided by the age when males were considered adults. The normalized ages enabled us to adjust for differences in the age when mountain gorillas and western gorillas reach adulthood (12 versus 14 years; see electronic supplementary material, §S2 for more life-history differences). Uncensored data points equalled the normalized age when males were separated from their mother, such as when the mother died or transferred to another group. Data points were censored when males reached adulthood with their mother, or at the normalized age when they were no longer observed, such as when they disappeared or the study ended. We used similar Cox models to calculate the probability that an immature male would remain in a group where the dominant

silverback was his putative father or any familiar male. See electronic supplementary material, §S3 for more probabilities to remain with potential relatives.

We used a generalized linear mixed model (GLMM, [54]) to compare the probability that males reached adulthood in a breeding group (versus a non-breeding group or solitary). The analysis used one data point for each male who reached adulthood during the study. The response variable equalled '1' if the male reached adulthood in a breeding group, and '0' if he did not. The predictor variable was the gorilla species. The model included the group ID as a random effect variable to control for multiple data points from the same groups. The model was run with a binomial error structure and logit link. See electronic supplementary material, §S4 for more details about the distribution of adult males in each species.

We ran an analysis of variance (ANOVA, [55]) to test whether the number of adult females per group is larger for mountain gorillas than western gorillas. The analysis used one data point for each breeding group in each study site. The predictor variable was the gorilla species. The response variable was the average number of adult females in the group. The average number of adult females in each group was calculated from its composition on the first day of each month when it was observed as a breeding group. To avoid excessive influence from groups with brief observations, each data point was weighted according to the number of months that the group was observed as a breeding group. The reported mean and standard deviation for the number of adult females were also weighted according to the number of months that the group was observed as a breeding group.

We used linear mixed models (LMM, [54]) to test whether the number of adult females per group is larger for multimale groups than one-male groups. The LMM used one data point for each group in each category (one-male versus multimale). The predictor variable was the group category. Some groups were observed in both categories, so we included the group ID as a random effect variable to control for multiple data points from the same group. The response variable was the average number of adult females while the group was in the category. The reported mean and standard deviation for the number of adult females were weighted according to the number of months that the group was observed in the category.

The Cox models were run using the 'coxme' function in R, and the ANOVA was performed with the 'lm' function (R Core Team 2016). We used the 'lmer' function in the 'lme4' package for the LMM and GLMM. To determine the p -values for the LMM and GLMM, we compared each full model with a reduced model in which the predictor variable had been removed.

3. Results

Male mountain gorillas had a 50% probability of reaching adulthood in a group with their mother, which is significantly higher than 18% for western gorillas (figure 1a; $z = 3.3$, $p < 0.001$). Of the 29 cases when an immature male mountain gorilla was separated from his mother, 45% occurred when the mother transferred to a known destination, 38% occurred when the mother died, 7% occurred when the mother disappeared, another 7% occurred during a group fission, and one case (3%) occurred when the male uncharacteristically transferred to another group (table 1). Transfers by the mother were also the primary cause for separations among western gorillas, but statistical comparisons of female dispersal in each population are confounded by unexplained disappearances (i.e. it is unknown whether some mothers had died or dispersed).

Male mountain gorillas had a 36% probability of reaching adulthood in a group where their putative father was still the dominant silverback, which is not significantly different from 61% for western gorillas (figure 1b; $z = 0.53$, $p = 0.59$). In all 12 cases, when subordinate male western gorillas reached adulthood with a dominant silverback who was not their putative father, the putative father had died (table 1). None of those dominant silverbacks was replaced by another familiar male, so the probabilities for immature male western gorillas to remain with a familiar dominant silverback were the same as the probabilities to remain with their putative father (figure 1b).

Male mountain gorillas had a 90% probability of reaching adulthood in a group where the dominant silverback was a familiar male, which is not significantly higher than 61% for western gorillas (figure 1b; $z = 1.7$, $p = 0.095$). Of the 40 cases when subordinate male mountain gorillas reached adulthood with a dominant silverback who was not their putative father, he was replaced by another familiar male in 35 cases (88%). The probability of having the putative father replaced with another familiar dominant silverback was significantly higher for mountain gorillas than for western gorillas (88% versus 0%, Fisher exact test, $p < 0.001$).

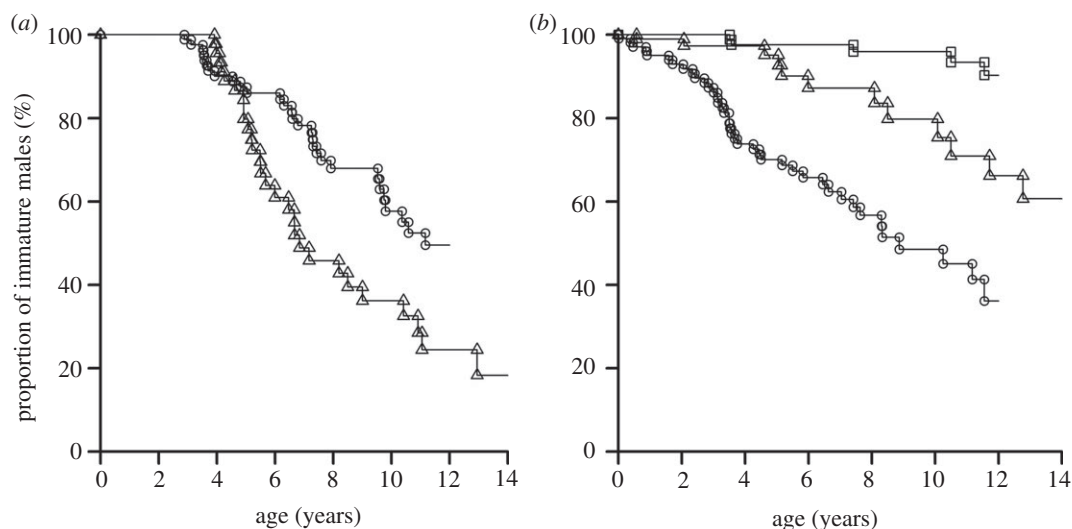


Figure 1. Probability for immature male mountain gorillas (circles) and western gorillas (triangles) to remain with their mother (a), or with the dominant silverback who was their putative father (b). In (b), squares show the probability for immature male mountain gorillas to remain with a dominant silverback who was ‘familiar’. With western gorillas, the results for familiar dominant silverbacks were identical to the results for putative fathers. Symbols are shown at the age of each censored data point, when an immature male was no longer with his potential relative.

Table 1. Causes for male gorillas to be separated from their mother, and to reach adulthood in a group where the dominant male was not their putative father or another familiar male. For example, in 45% of the 29 cases when a male mountain gorilla was separated from his mother, the mother had dispersed from the group.

| species | mountain gorillas | western gorillas | mountain gorillas | western gorillas | mountain gorillas | western gorillas |
|----------------------------|-------------------|------------------|-------------------|------------------|-------------------|------------------|
| potential relative | mother | mother | putative father | putative father | familiar male | familiar male |
| <i>cause of separation</i> | | | | | | |
| adult dispersal | 45% | 50% | | | | |
| adult death | 38% | | 58% | 100% | 60% | 100% |
| adult disappearance | 7% | 39% | | | 20% | |
| group fission | 7% | | 18% | | | |
| group disintegration | | 11% | | | | |
| dominance usurpation | | | 23% | | | |
| immature dispersal | 3% | | 3% | | 20% | |
| total separations | 29 | 28 | 40 | 12 | 5 | 12 |

Only 46% of 54 male western gorillas were in a breeding group when they reached adulthood, which is significantly lower than 83% of 47 male mountain gorillas ($\chi^2 = 5.3$, d.f. = 1, $p = 0.021$). Immigration was the main pathway into non-breeding groups for immature male western gorillas, as expected when one-male breeding groups disintegrate after the death of the dominant silverback. See electronic supplementary material, S55 for more details about the typical life cycle of gorilla groups.

Mountain gorilla groups contained a weighted average of 5.1 ± 2.7 adult females, which is significantly higher than 3.6 ± 1.5 females for western gorillas ($R^2 = 11.6\%$, $F_{56,1} = 7.4$, $p = 0.0087$). Among mountain gorillas, the weighted average number of adult females was 5.3 ± 3.2 for multimale groups, which is not significantly higher than 4.9 ± 2.6 for one-male groups ($\chi^2 = 1.8$, d.f. = 1, $p = 0.18$). Among western gorillas, the weighted average number of adult females was 1.6 ± 0.67 for multimale groups, which is significantly lower than 3.8 ± 1.5 for one-male groups ($\chi^2 = 10.2$, d.f. = 1, $p < 0.001$). The results for western gorillas are in the opposite direction of expectations, and they arose because groups typically became multimale when the dominant male was old and many of the females had already left.

4. Discussion

Variations in the distributions of adult males and females have been attributed to many factors including the distribution of food and other resources, the degree of reproductive synchrony among females, kin competition and cooperation, predation and infanticide, life-history traits and inbreeding [17,25,56]. This study has found significant evidence for a novel theory about distribution of the males: female mountain gorillas remain with their sons for longer than western gorillas, which may lead to greater male philopatry and a higher proportion of multimale groups among mountain gorillas [38,39,47]. We also found limited support for the socio-ecological theory that the number of adult males per group is influenced by the distribution of adult females [57,58]. Collectively, our results highlight the potentially far-reaching consequences of maternal support that extends beyond infancy, and they illustrate the opportunity to incorporate additional factors into comparative studies of variations in social organization among primates and other species [7,59,60].

4.1. Presence of the mother and other potential relatives

The probability for males to reach adulthood in the same group with their mother was significantly higher for mountain gorillas than for western gorillas. Male mountain gorillas are significantly more philopatric when their mother is present, perhaps because her proximity facilitates their ability to develop relationships with other females and with the dominant silverback [38,47]. Similarly, northern muriqui mothers (*Brachyteles hypoxanthus*) may help their sons gain access to other adult females, and chacma baboons mothers (*Papio ursinus*) may promote closer paternal relationships for their sons [15,20]. Maternal support may help male hyenas (*Crocuta crocuta*) to secure more favourable dispersal destinations, whereas the more favourable strategy for many male mountain gorillas seems to be philopatry rather than dispersal [14,46,61]. If the presence of the mother can influence the dispersal patterns and social organization among mountain gorillas, then it could also account for differences between mountain gorillas versus western gorillas. One distinction is that essentially all western male gorillas emigrate, even though some of them reach adulthood in the same group with their mother [39]. Western gorillas may have more diffuse spacing within their groups, so even if a male can remain with his mother, he might not gain much access to other group members [62]. Thus, the western male gorillas do not seem to exhibit conditional dispersal that is observed in mountain gorillas and many other species [63,64].

Owing to the limitations in distinguishing between death and dispersal in this study, it is difficult to determine the proximate cause for the differences in the presence of the mother. Hypothetically, the prolonged presence of mothers among mountain gorillas could indicate that they have lower mortality than female western gorillas, but such results would not be consistent with evidence of a slower life history for western gorillas [65–67]. Instead, the prolonged presence of mothers among mountain gorillas is more likely to indicate that they disperse less frequently than parous western gorillas [35,36,68]. Such a distinction would be consistent with findings that female mountain gorillas have lower dispersal rates from multimale groups than from one-male groups, perhaps due to lower risks of infanticide in multimale groups [37,41,69,70]. If so, then a positive feedback loop may develop that increases the proportion of multimale groups among mountain gorillas: an initial formation of multimale groups could reduce the rate of female dispersal, which should enable more sons to reach adulthood with their mothers, which could lead to greater male philopatry and a higher proportion of multimale groups.

Mountain gorillas and western gorillas did not differ significantly in the probability for males to reach adulthood in a group where the dominant silverback was their putative father or another familiar male. Further study is needed to determine whether such relationships can affect whether male mountain gorillas will emigrate or remain philopatric, but the presence of the actual father has not shown any significant effect on dispersal [38,40,46]. Such relationships do not seem to promote philopatry among western gorillas either, because essentially all subordinate males emigrate, even though 68% of them reached adulthood with their putative father as the dominant silverback [39]. Yet even if familiar dominant silverbacks do not promote philopatry among male western gorillas, the end of familiar relationships can lead to involuntary dispersal as reported for Siberian jays (*Perisoreus infaustus*), lions (*Panthera leo*), snub-nosed langurs (*Rhinopithecus* spp.) and other species [13,71,72]. Involuntary dispersal may reduce the probability that male western gorillas reach adulthood in a breeding group, which was significantly lower than the corresponding probability for mountain gorillas in this study [35,42]. The maturation of natal males is the primary mechanism for multimale breeding groups to form, so

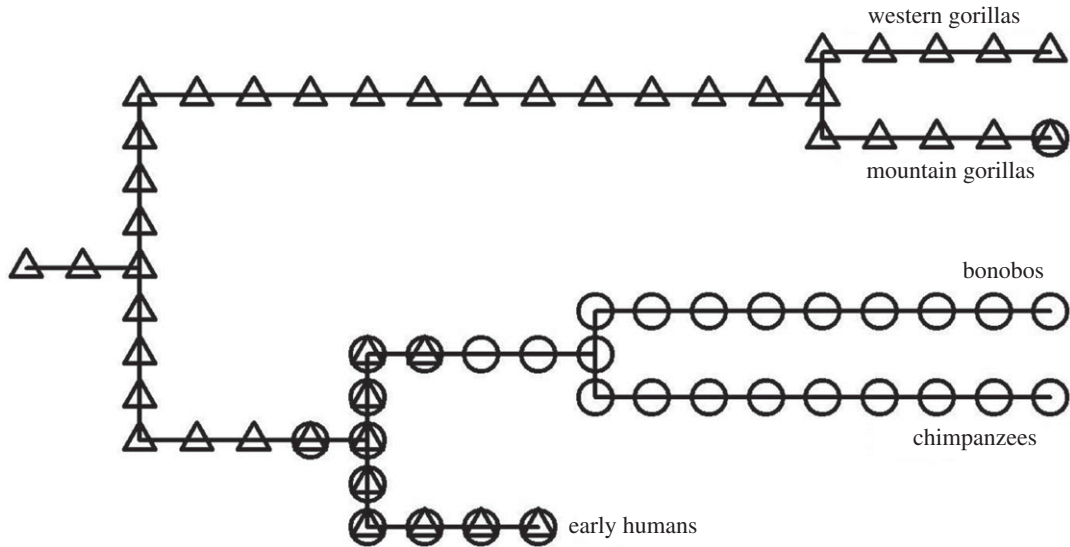


Figure 2. Proposed evolution of male philopatry among Homininae (*Gorilla*, *Pan* and *Homo*). Triangles represent species with predominantly male dispersal, circles indicate philopatry and overlapping symbols reflect a combination of both strategies. The phylogenetic perspective assumes that the trait shared by closely related species was also present in their last common ancestor. The assumption minimizes the number of times that male philopatry would have evolved independently.

involuntary dispersal may help to explain why such groups are less common among western gorillas than mountain gorillas [40,73].

4.2. Variations in social organization

Socio-ecological models predict that the distribution of males will reflect the distribution of females, and those predictions have been supported by phylogenetic analyses of primates [6,7,59]. Our comparisons between species were also consistent with such predictions, because mountain gorillas had significantly more adult females per group and a higher proportion of multimale groups than western gorillas. One potential caveat is that the difference between species was relatively small in comparison with the variance within species ($R^2 = 11.6\%$), which could help to explain why previous comparisons have not been statistically significant [43,45]. Furthermore, the socio-ecological theory was not supported by our comparisons of social organization within either species, because multimale groups did not have more adult females than one-male groups. Similarly, other studies have found weaker correlations within populations than between species [5,74,75]. Within such populations, variations in social organization may reflect different stages in the life cycle of groups, rather than differences in male reproductive strategies [51,74,76]. Correlations between the distributions of males versus females may also be weakened within populations with high variability in male quality, high dispersal costs and/or limited ability for males to assess reproductive opportunities [5,70,77]. Further study of those influences within species may help to refine our understanding of variations in social organization among species, especially when male dispersal is limited.

4.3. Evolution of Homininae (*Gorilla*, *Pan* and *Homo*)

The increased proportion of multimale groups has been considered a recent development in the evolutionary history of mountain gorillas, because they lack physiological traits that are typically associated with multimale mating systems [78,79]. If so, then mothers may have facilitated the evolution from the nearly universal dispersal of male western gorillas to the context-dependent philopatry of male mountain gorillas (figure 2). A similar evolution may have gone further for chimpanzees and bonobos, whose multimale social organizations arise from more consistent male philopatry than mountain gorillas [80,81]. Maternal support of sons can extend beyond infancy in both of those *Pan* species, and their parous females disperse less often than gorillas, which increases the probability that the mother will remain present [16,38,82].

The social system of early humans remains unclear, but their degree of male philopatry is often considered greater than western gorillas, and possibly as extreme as the *Pan* species [30,32,83–85]. If

so, then male philopatry could have been developing in the last common ancestor of *Pan* and *Homo* when those taxa diverged, even if it subsequently continued further in *Pan* (for additional possibilities, see [31,86]). Thus, the extended maternal support of sons may have contributed to the development of male philopatry for humans and our closest extant relatives.

Ethics. This research involved non-invasive work with wild non-human primates. All work was done in accordance with guidelines of the national authorities where the work occurred.

Data accessibility. Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.90nc6> [87]. Additional information is included in the electronic supplementary material.

Authors' contributions. M.G., T.B., M.M., E.J.S., P.U., I.M. and E.K. acquired the data. A.M.R., T.B., M.M. and M.M.R. contributed to the conception and design of the study, as well as the interpretation of data. A.M.R. performed the analyses and drafted the manuscript. All authors revised the manuscript, gave final approval for publication, and agreed to be accountable for the work (except for E.K. who is deceased).

Competing interests. We have no competing interests.

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References

- Pereira ME, Clutton-Brock TH, Kappeler PM. 2000 Understanding male primates. In *Primate males* (ed. PM Kappeler), pp. 271–277. Cambridge, UK: Cambridge University Press.
- Eisenberg JF, Muckenhirn NA, Rudran R. 1972 Relation between ecology and social structure in primates. *Science* **176**, 863–864. (doi:10.1126/science.176.4037.863)
- Crook JH, Gartlan JS. 1966 Evolution of primate societies. *Nature* **210**, 1200–1203. (doi:10.1038/2101200a0)
- Altmann J. 1990 Primate males go where the females are. *Anim. Behav.* **39**, 193–195. (doi:10.1016/S0003-3472(05)80740-7)
- Altmann J. 2000 Models of outcome and process: predicting the number of males in primate groups. In *Primate males* (ed. PM Kappeler), pp. 236–247. Cambridge, UK: Cambridge University Press.
- Lindenfors P, Froberg L, Nunn CL. 2004 Females drive primate social evolution. *Proc. R. Soc. Lond. B* **271**, S101–S103. (doi:10.1098/rsbl.2003.0114)
- Carnes LM, Nunn CL, Lewis RJ. 2011 Effects of the distribution of female primates on the number of males. *PLoS ONE* **6**, e19853. (doi:10.1371/journal.pone.0019853)
- van Schaik C, Janson C. 2000 *Infanticide by males and its implications*, 316. Cambridge, UK: Cambridge University Press.
- van Schaik CP, Kappeler PM. 1997 Infanticide risk and the evolution of male-female association in primates. *Proc. R. Soc. Lond. B* **264**, 1687–1694. (doi:10.1098/rspb.1997.0234)
- Devillard S, Allaine D, Gaillard JM, Pontier D. 2004 Does social complexity lead to sex-biased dispersal in polygynous mammals? A test on ground-dwelling sciurids. *Behav. Ecol.* **15**, 83–87. (doi:10.1093/beheco/arg099)
- Jack KM, Isbell LA. 2009 Dispersal in primates: advancing an individualized approach. *Behaviour* **146**, 429–436. (doi:10.1163/156853909X410612)
- Strier KB. 2008 The effects of kin on primate life histories. *Annu. Rev. Anthropol.* **37**, 21–36. (doi:10.1146/annurev.anthro.37.081407.085218)
- Elliot NB, Valeix M, Macdonald DW, Loveridge AJ. 2014 Social relationships affect dispersal timing revealing a delayed infanticide in African lions. *Oikos* **123**, 1049–1056. (doi:10.1111/oik.01266)
- Hoener OP, Wachter B, Hofer H, Wilhelm K, Thierer D, Trillmich F, Burke T, East ML. 2010 The fitness of dispersing spotted hyaena sons is influenced by maternal social status. *Nat. Commun.* **1**, 1–7. (doi:10.1038/ncomms1059)
- Strier KB, Chaves PB, Mendes SL, Fagundes V, Di Fiore A. 2011 Low paternity skew and the influence of maternal kin in an egalitarian, patrilocal primate. *Proc. Natl Acad. Sci. USA* **108**, 18 915–18 919. (doi:10.1073/pnas.1116737108)
- Surbeck M, Mundry R, Hohmann G. 2011 Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). *Proc. R. Soc. B* **278**, 590–598. (doi:10.1098/rspb.2010.1572)
- 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. (doi:10.1098/rstb.2012.0348)
- Hawkes K. 2004 Human longevity—the grandmother effect. *Nature* **428**, 128–129. (doi:10.1038/428128a)
- Bogin B. 2009 Childhood, adolescence, and longevity: a multilevel model of the evolution of reserve capacity in human life history. *Am. J. Hum. Biol.* **21**, 567–577. (doi:10.1002/ajhb.20895)
- Huchard E, Charpentier MJ, Marshall H, King AJ, Knapp LA, Cowlshaw G. 2013 Paternal effects on access to resources in a promiscuous primate society. *Behav. Ecol.* **24**, 229–236. (doi:10.1093/beheco/ars158)
- Charpentier MJE, Van Horn RC, Altmann J, Alberts SC. 2008 Paternal effects on offspring fitness in a multimale primate society. *Proc. Natl Acad. Sci. USA* **105**, 1988–1992. (doi:10.1073/pnas.0711219105)
- Jack KM, Fedigan L. 2004 Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 1: patterns and causes of natal emigration. *Anim. Behav.* **67**, 761–769. (doi:10.1016/j.anbehav.2003.04.015)
- Schoof VAM, Jack KM, Isbell LA. 2009 What traits promote male parallel dispersal in primates? *Behaviour* **146**, 701–726. (doi:10.1163/156853908X399086)
- Waser PM, Austad SN, Keane B. 1986 When should animals tolerate inbreeding. *Am. Nat.* **128**, 529–537. (doi:10.1086/284585)
- Perrin N, Mazalov V. 2000 Local competition, inbreeding, and the evolution of sex-biased

- dispersal. *Am. Nat.* **155**, 116–127. (doi:10.1086/303296)
26. Handley LJJ, Perrin N. 2007 Advances in our understanding of mammalian sex-biased dispersal. *Mol. Ecol.* **16**, 1559–1578. (doi:10.1111/j.1365-294X.2006.03152.x)
27. Lukas D, Clutton-Brock TH. 2011 Group structure, kinship, inbreeding risk and habitual female dispersal in plural-breeding mammals. *J. Evol. Biol.* **24**, 2624–2630. (doi:10.1111/j.1420-9101.2011.02385.x)
28. Clutton-Brock T, Janson C. 2012 Primate socioecology at the crossroads: past, present, and future. *Evol. Anthropol.* **21**, 136–150. (doi:10.1002/evan.21316)
29. Lockwood CA, Menter CG, Moggi-Cecchi J, Keyser AW. 2007 Extended male growth in a fossil hominid species. *Science* **318**, 1443–1446. (doi:10.1126/science.1149211)
30. Koenig A, Borries C. 2012 Hominoid dispersal patterns and human evolution. *Evol. Anthropol.* **21**, 108–112. (doi:10.1002/evan.21300)
31. Chapais B. 2013 Monogamy, strongly bonded groups, and the evolution of human social structure. *Evol. Anthropol.* **22**, 52–65. (doi:10.1002/evan.21345)
32. Duda P, Zrzavy J. 2013 Evolution of life history and behavior in Hominidae: towards phylogenetic reconstruction of the chimpanzee-human last common ancestor. *J. Hum. Evol.* **65**, 424–446. (doi:10.1016/j.jhevol.2013.07.009)
33. Harcourt AH, Stewart KS, Fossey D. 1976 Male emigration and female transfer in wild mountain gorilla. *Nature* **263**, 226–227. (doi:10.1038/263226a0)
34. Harcourt AH. 1978 Strategies of emigration and transfer by primates, with particular reference to gorillas. *J. Comp. Ethol.* **48**, 401–420. (doi:10.1111/j.1439-0310.1978.tb00267.x)
35. Stokes EJ, Parnell RJ, Olejniczak C. 2003 Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Behav. Ecol. Sociobiol.* **54**, 329–339. (doi:10.1007/s00265-003-0630-3)
36. Robbins AM, Stoinski T, Fawcett K, Robbins MM. 2009 Leave or conceive: natal dispersal and philopatry of female mountain gorillas in the Virunga volcano region. *Anim. Behav.* **77**, 831–838. (doi:10.1016/j.anbehav.2008.12.005)
37. Robbins AM, Stoinski TS, Fawcett KA, Robbins MM. 2009 Socioecological influences on the dispersal of female mountain gorillas—evidence of a second folivore paradox. *Behav. Ecol. Sociobiol.* **63**, 477–489. (doi:10.1007/s00265-008-0679-0)
38. Stoinski TS, Vecellio V, Ngaboyamahina T, Ndagijimana F, Rosenbaum S, Fawcett KA. 2009 Proximate factors influencing dispersal decisions in male mountain gorillas, *Gorilla beringei beringei*. *Anim. Behav.* **77**, 1155–1164. (doi:10.1016/j.anbehav.2008.12.030)
39. 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. (doi:10.1002/ajp.20069)
40. Robbins MM. 1995 A demographic analysis of male life history and social structure of mountain gorillas. *Behaviour* **132**, 21–47. (doi:10.1163/156853995X00261)
41. 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. (doi:10.1371/journal.pone.0078256)
42. Watts DP. 1989 Infanticide in mountain gorillas—new cases and a reconsideration of the evidence. *Ethology* **81**, 1–18. (doi:10.1111/j.1439-0310.1989.tb00754.x)
43. Harcourt AH, Stewart KJ. 2007 *Gorilla society: conflict, compromise, and cooperation between the sexes*, 459. Chicago, IL: University of Chicago Press.
44. Robbins MM. 2010 Gorillas: diversity in ecology and behavior. In *Primates in perspective* (eds CJ Campbell, A Fuentes, KC MacKinnon, SK Bearder, RM Stumpf), pp. 326–339. Oxford, UK: Oxford University Press.
45. Yamagiwa J, Kahekwa J, Basabose AK. 2003 Intra-specific variation in social organization of gorillas: implications for their social evolution. *Primates* **44**, 359–369. (doi:10.1007/s10329-003-0049-5)
46. Watts DP. 2000 Causes and consequences of variation in male mountain gorilla life histories and group membership. In *Primate males* (ed. PM Kappeler), pp. 169–180. Cambridge, UK: Cambridge University Press.
47. Harcourt AH. 1981 Intermale competition and the reproductive behavior of the great apes. In *Reproductive biology of the great apes* (ed. CE Graham), pp. 301–318. New York, NY: Academic Press.
48. Rosenbaum S, Silk JB, Stoinski TS. 2011 Male-immature relationships in multi-male groups of mountain gorillas (*Gorilla beringei beringei*). *Am. J. Primatol.* **73**, 356–365. (doi:10.1002/ajp.20905)
49. Robbins AM, Gray M, Basabose A, Uwingeli P, Mburanumwe I, Kagoda E, Robbins MM. 2014 Variance in the reproductive success of dominant male mountain gorillas. *Primates* **55**, 489–499. (doi:10.1007/s10329-014-0426-2)
50. Parnell R. 2002 *The social structure and behaviour of western lowland gorillas (Gorilla gorilla gorilla) at Mbeli Bai, Republic of Congo, Department of Psychology*, 429. Stirling, UK: University of Stirling.
51. 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. (doi:10.1002/ajp.1074)
52. Breuer T. 2008 *Male reproductive success in wild western gorillas (Gorilla gorilla)*, Max Planck Institute for Evolutionary Anthropology, 129. Leipzig, Germany: University of Leipzig.
53. Pankratz VS, de Andrade M, Therneau TM. 2005 Random-effects Cox proportional hazards model: general variance components methods for time-to-event data. *Genet. Epidemiol.* **28**, 97–109. (doi:10.1002/gepi.20043)
54. Jiang J. 2007 *Linear and generalized linear mixed models and their applications*, 257. Berlin, Germany: Springer.
55. Sokal R, Rohlf F. 1995 *Biometry*, 3rd edn. New York, NY: W. H. Freeman and Company.
56. Clutton-Brock TH, Lukas D. 2012 The evolution of social philopatry and dispersal in female mammals. *Mol. Ecol.* **21**, 472–492. (doi:10.1111/j.1365-294X.2011.05232.x)
57. Wrangham RW. 1980 An ecological model of female-bonded primate groups. *Behaviour* **75**, 262–300. (doi:10.1163/156853980X00447)
58. Clutton-Brock TH. 1989 Mammalian mating systems. *Proc. R. Soc. Lond. B* **236**, 339–372. (doi:10.1098/rspb.1989.0027)
59. Nunn CL. 1999 The number of males in primate social groups: a comparative test of the socioecological model. *Behav. Ecol. Sociobiol.* **46**, 1–13. (doi:10.1007/s002650050586)
60. Mitani JC, Gros-Louis J, Manson JH. 1996 Number of males in primate groups: comparative tests of competing hypotheses. *Am. J. Primatol.* **38**, 315–332. (doi:10.1002/(SICI)1098-2345(1996)38:4<315::AID-AJP3>3.0.CO;2-1)
61. Robbins AM, Robbins MM. 2005 Fitness consequences of dispersal decisions for male mountain gorillas (*Gorilla beringei beringei*). *Behav. Ecol. Sociobiol.* **58**, 295–309. (doi:10.1007/s00265-005-0917-7)
62. Salmi R, Doran-Sheehy DM. 2014 The function of loud calls (hoot series) in wild western gorillas (*Gorilla gorilla*). *Am. J. Phys. Anthropol.* **155**, 379–391. (doi:10.1002/ajpa.22575)
63. Bach LA, Ripa J, Lundberg P. 2007 On the evolution of conditional dispersal under environmental and demographic stochasticity. *Evol. Ecol. Res.* **9**, 663–673.
64. Poethke HJ, Weisser WW, Hovestadt T. 2010 Predator-induced dispersal and the evolution of conditional dispersal in correlated environments. *Am. Nat.* **175**, 577–586. (doi:10.1086/651595)
65. Charnov EL. 1993 *Life history invariants. Oxford series in ecology and evolution*, 168. Oxford, UK: Oxford University Press.
66. Breuer T, Hockemba MBN, Olejniczak C, Parnell RJ, Stokes EJ. 2009 Physical maturation, life-history classes and age estimates of free-ranging western gorillas: insights from Mbeli Bai, Republic of Congo. *Am. J. Primatol.* **71**, 106–119. (doi:10.1002/ajp.20628)
67. Robbins MM, Gray M, Kagoda E, Robbins AM. 2009 Population dynamics of the Bwindi mountain gorillas. *Biol. Conserv.* **142**, 2886–2895. (doi:10.1016/j.biocon.2009.07.010)
68. Sicotte P. 2001 Female mate choice in mountain gorillas. In *Mountain gorillas: three decades of research at Karisoke* (eds M Robbins, P Sicotte, K Stewart), pp. 59–88. Cambridge, UK: Cambridge University Press.
69. Janson CH, van Schaik CP. 2000 The behavioral ecology of infanticide by males. In *Infanticide by males and its implications* (eds CH Janson, CP van Schaik), pp. 469–494. Cambridge, UK: Cambridge University Press.
70. Pradhan GR, van Schaik C. 2008 Infanticide-driven intersexual conflict over matings in primates and its effects on social organization. *Behaviour* **145**, 251–275. (doi:10.1163/156853907783244710)
71. Ekman J, Griesser M. 2002 Why offspring delay dispersal: experimental evidence for a role of parental tolerance. *Proc. R. Soc. Lond. B* **269**, 1709–1713. (doi:10.1098/rspb.2002.2082)
72. Ren B, Li D, He X, Qiu J, Li M. 2011 Female resistance to invading males increases infanticide in langurs. *PLoS ONE* **6**, e18971. (doi:10.1371/journal.pone.0018971)
73. Robbins MM, Robbins AM. 2004 Simulation of the population dynamics and social structure of the

- Virunga mountain gorillas. *Am. J. Primatol.* **63**, 201–223. (doi:10.1002/ajp.20052)
74. Sterck EHM, van Hooff JARAM. 2000 The number of males in langur groups: monopolizability of females or demographic processes? In *Primate males* (ed. PM Kappeler), pp. 120–129. Cambridge, UK: Cambridge University Press.
75. Pochron ST, Wright PC. 2003 Variability in adult group compositions of a prosimian primate. *Behav. Ecol. Sociobiol.* **54**, 285–293. (doi:10.1007/s00265-003-0634-z)
76. Dunbar RIM, Dunbar EP. 1976 Contrasts in social-structure among black-and-white colobus monkey groups. *Anim. Behav.* **24**, 84–92. (doi:10.1016/S0003-3472(76)80102-9)
77. Breuer T, Robbins AM, Boesch C, Robbins MM. 2012 Phenotypic correlates of male reproductive success in western gorillas. *J. Hum. Evol.* **62**, 466–472. (doi:10.1016/j.jhevol.2012.01.006)
78. Harcourt AH, Harvey PH, Larson SG, Short RV. 1981 Testis weight, body-weight and breeding system in primates. *Nature* **293**, 55–57. (doi:10.1038/293055a0)
79. Nunn CL. 1999 The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Anim. Behav.* **58**, 229–246. (doi:10.1006/anbe.1999.1159)
80. Stumpf R. 2007 Chimpanzees and bonobos: diversity within and between species. In *Primates in perspective* (eds CJ Campbell, A Fuentes, KC MacKinnon, M Panger, SK Bearder), pp. 321–344. Oxford, UK: Oxford University Press.
81. Watts DP. 2012 The apes: taxonomy, biogeography, life histories, and behavioral ecology. In *The evolution of primate societies* (eds J Mitani, J Call, PM Kappeler, RA Palombit, JB Silk), pp. 113–142. Chicago, IL: University of Chicago Press.
82. Schubert G, Vigilant L, Boesch C, Klenke R, Langergraber K, Mundry R, Surbeck M, Hohmann G. 2013 Co-residence between males and their mothers and grandmothers is more frequent in bonobos than chimpanzees. *PLoS ONE* **8**, e83870. (doi:10.1371/journal.pone.0083870)
83. Yamagiwa J. 2015 Evolution of hominid life history strategy and origin of human family. In *Dispersing primate females: life history and social strategies in male-philopatric species* (eds T Furuichi, J Yamagiwa, F Aureli), pp. 255–285. Tokyo, Japan: Springer-Verlag.
84. Copeland SR, Sponheimer M, de Ruiter DJ, Lee-Thorp JA, Codron D, Roux PJ, Grimes V, Richards MP. 2011 Strontium isotope evidence for landscape use by early hominins. *Nature* **474**, 76–78. (doi:10.1038/nature10149)
85. Lalueza-Fox C *et al.* 2011 Genetic evidence for patrilocality mating behavior among Neandertal groups. *Proc. Natl Acad. Sci. USA* **108**, 250–253. (doi:10.1073/pnas.1011553108)
86. Chapais B. 2011 The deep social structure of humankind. *Science* **331**, 1276–1277. (doi:10.1126/science.1203281)
87. Robbins AM, Gray M, Breuer T, Manguette M, Stokes EJ, Uwingeli P, Mburanumwe I, Kagoda E, Robbins MM. 2016 Data from: Mothers may shape the variations in social organization among gorillas. Dryad Digital Repository. (doi:10.5061/dryad.90nc6)