PROCEEDINGS B

THE ROYAL SOCIETY PUBLISHING

Conditional fetal and infant killing by male baboons

Matthew N. Zipple[1], Jackson H. Grady[1], Jacob B. Gordon[1], Lydia D. Chow[1], Elizabeth A. Archie[3,4], Jeanne Altmann[4,5] and Susan C. Alberts[1,2,4]

[1]Department of Biology, and [2]Department of Evolutionary Anthropology, Duke University, Durham, NC, USA
[3]Department of Biological Sciences, University of Notre Dame, Notre Dame, IN, USA
[4]Institute of Primate Research, National Museums of Kenya, Nairobi, Kenya
[5]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA

MNZ, 0000-0003-3451-2103

Sexually selected feticide—the death of infants *in utero* as a result of male behaviour—has only rarely been described or analysed, although it is presumed to be favoured by the same selective pressures that favour sexually selected infanticide. To test this hypothesis, we measured the frequency of feticide and infanticide by male baboons of the Amboseli basin in Kenya, and examined which characteristics of a male and his environment made him more likely to commit feticide and/or infanticide. We found a dramatic increase in fetal and infant death rates, but no increase in death rates of 1- to 2-year-old individuals, following the immigration of males who stood to benefit from feticide and infanticide. Specifically, fetal and infant death rates were highest following immigrations in which: (i) the immigrant male rapidly attained high rank, (ii) that male remained consistently resident in the group for at least three months, (iii) food availability and social group range overlap was relatively low and (iv) relatively many pregnant females and/or dependent infants were present. Together, these results provide strong evidence for the existence of both sexually selected feticide and infanticide in our population, and they indicate that feticide and infanticide are conditional male behavioural strategies employed under particular circumstances.

1. Introduction

Sexually selected feticide and infanticide are behaviours that involve spontaneous abortions and the death of infants as a result of male behaviour, yield reproductive benefits to those same males and alter population structures. Infanticide has been the subject of dozens of studies in wild animal populations [1] and has been discussed as an important mechanism in the evolution of primate sociality in particular [2–8]. By contrast, studies of feticide are very rare. Within primates, case studies of apparent sexually selected feticide have previously been described in savannah baboons from Amboseli [7,9,10] and in langurs at Jodhpur [11–13], but no long-term study has quantitatively assessed the population-wide prevalence of sexually selected feticide.

The sexual selection hypothesis for infanticide [14,15] posits that males derive a fitness benefit from killing infants by accelerating the return of lactating females to ovulatory cycling. This hypothesis yields three main predictions: (i) that infants will be killed by unrelated males, (ii) that inter-birth intervals of mothers of infants that are killed will be shorter than they would be in the absence of infanticide and (iii) that infanticidal males are likely to mate with infants' mothers following infant death [16]. Among mammals, sexually selected infanticide has been documented in lions [17], cetaceans [18,19], murid rodents [20] and especially in primates, where support for the sexual selection hypothesis has been found in 84 populations of 54 species of primates [1]. In both single-male and multi-male social groups, infanticide is most often committed by recently immigrated males (e.g. ursine colobus monkeys: [21]; chacma baboons: [22]). The frequency

of infanticide varies within and across populations of a given species, but sources of variance in the frequency of infanticide are poorly understood [22–24].

Males will experience selection to reduce waiting time for reproductive opportunities. By killing an infant, an infanticidal male causes the infant's mother to return to a reproductive state sooner than she otherwise would by eliminating a period of continued lactation during which she would not be cycling. A feticidal male gains even greater reproductive benefits, as he is able to eliminate periods of both pregnancy and lactation. Feticide and infanticide can be considered closely related phenomena, differing primarily in the stage of development at which the developing offspring dies [8]. In a social group in which both feticide and infanticide are possible, committing feticide provides a male with greater reproductive benefits than does committing infanticide, and committing both feticide and infanticide creates greater reproductive opportunity still (see electronic supplementary material, figure S1).

Importantly, sexually selected feticide is related to, but distinct from, the Bruce effect—a phenomenon in which pregnant females spontaneously terminate their pregnancies following their exposure to a non-paternal breeding male [25,26]. Direct or indirect evidence of a Bruce effect has been documented in captive rodents, [27], lions [28] and gelada monkeys [29]. Notably, a recent study identified a Bruce effect in domestic horses [30], leading to the suggestion that previous studies suggesting sexually selected feticide in equids [31,32] were instead documenting a Bruce effect [29,30].

Under a Bruce effect, physical contact with the non-paternal male is not necessary to induce abortion. In the case of rodents, chemical signals have been demonstrated to be the proximate mechanisms for pregnancy termination [33–35]. Because the Bruce effect is mediated by signals that are readily received by all females in a population, the Bruce effect tends to yield very high rates of abortion following the replacement of a breeding male (for example, termination of 71–76% of pregnancies in mice [25], 81% of early pregnancies in prairie voles [36], 100% of early pregnancies in wild horses [32] and 80% of pregnancies in geladas [29]). In populations in which a Bruce effect is acting, abortion appears to be an obligate response to exposure to a non-paternal, breeding male.

Unlike the Bruce effect, sexually selected feticide is induced by male aggression (electronic supplementary material, figure S2). Females that terminate their pregnancy following trauma do so as a result of damage that has been inflicted on them or their fetus [37]. Following the immigration of a feticidal male, some females experience fetal loss, but many others do not. Sexually selected feticide is defined as fetal loss that occurs only when specific females are successfully targeted by feticidal males, and therefore constitutes a facultative female response to exposure to a non-parental male.

We tested for the presence of both feticide and infanticide in the Amboseli population of savannah baboons by comparing rates of fetal and infant death immediately before and after the immigration of adult males who stood to benefit most from feticide or infanticide [38]. We also tested whether the patterns of feticide and infanticide we detected support the predictions of the sexual selection hypothesis, and whether feticide and infanticide are contingent male behavioural strategies that depend on the reproductive environment in which he lives.

2. Material and methods

(a) Study area

The Amboseli Baboon Research Project is a long-term longitudinal study of a population of baboons in an East African semi-arid short-grass savannah with interspersed woodland [39] in and near Amboseli National Park, Kenya. A detailed description of the study system can be found elsewhere [38]. Behavioural, environmental and demographic data have been continuously collected from the population since 1971. All subjects are recognized visually on sight. A census is conducted every time an observer is with a group, allowing us to detect, during each observation day, the presence or absence of all group members, including which adult males are in the groups being observed that day.

The near-daily observation of groups allows for the precise assignment of infant birth and death dates, as well as conception dates and fetal loss dates. For these latter dates, we rely on a well-developed method that has been consistently employed throughout the study period [40]. This method combines menstruation, sex skin swelling and bleeding data as well as changes in the colour of the paracallosal skin [41], and allows for the precise assignment of pregnancy start and end dates for females in our population. Endocrinological analyses from our study population, combined with decades of close observation, confirm that these visual methods are greater than 97% accurate for identifying the timing of the onset of pregnancy [40]. Male dominance ranks are assigned monthly for all males in a group based on wins and losses in dyadic agonistic interactions between males. Males are taken to be winners of an agonistic interaction if they give only non-submissive gestures while their opponent gives only submissive gestures [42].

The number of study groups has fluctuated over the course of the study as groups have fissioned or occasionally fused, and has varied from 1 to 6 at any given time. Some groups have been dropped for logistical reasons and others maintained as study groups. In the late 1980s and early 1990s, our two original study groups, Alto's and Hook's, initiated a home range shift from an area of low social group overlap and relatively poor habitat to an area of higher resource availability and higher social group overlap [39,43,44]. For Alto's Group, periods of low resource availability occurred from 1971 to 1987, and for Hook's Group, low resource availability occurred from 1980 to 1991 [43]. During these time periods, baboon groups were relatively spread out from each other. As a result, males often spent considerable time alone between leaving one group and entering a new one, making immigration relatively more costly [45]. The home range shifts were associated with changes in social and foraging behaviours [39] and with an increase in population growth rate.

(b) Detecting feticide and infanticide

Feticide and infanticide can be difficult to directly observe in natural animal populations, especially if they are relatively uncommon. Infanticidal attacks are generally quite swift, making it easy for observers to miss them [11,22]. In the case of feticide, instances of fetal loss can be difficult to trace to male attacks on pregnant females in the absence of extremely intensive and detailed behavioural observations. This is true even in species in which pregnancy and fetal loss can be relatively easily observed such as baboons, in which females have external indicators of reproductive status and pregnancy that allow researchers to identify pregnancies with a high degree of accuracy [40,41].

This study includes no direct observations of feticide or infanticide or behavioural evidence of male aggression. Instead, we measured the frequency of feticide and infanticide by comparing fetal and infant death rates immediately before and after male immigrations. Specifically, for a set of immigrations

of adult males into baboon study groups in Amboseli, we used Fisher's exact test to compare the rates of fetal and infant deaths in the destination groups in the two weeks prior to each immigration to rates in the two weeks after each immigration. A systematic increase in fetal and infant death rates in the two weeks following male immigrations would indicate the presence of feticide and infanticide. We considered infants to be individuals less than 1-year old. In Amboseli, 60% of females have resumed sexual cycling by the time their offspring reaches 1 year of age, and 95% have resumed by the time their offspring reaches 1.4 years of age.

The narrow time window of our analysis (two weeks before and after immigrations), coupled with a lack of seasonality in immigrations in this population, help to rule out the possibility that an increase in fetal and/or infant death rates could be explained by coincidental increases in male immigration immediately prior to the systematic occurrence of fetal and infant deaths from other causes. To further confirm that any increase in fetal and infant death was linked to male immigrations, we also compared fetal and infant death rates in the groups into which males immigrated to rates in groups into which males did not immigrate over the same time period.

We reasoned that some immigrations were more likely to result in feticide or infanticide than others. High-ranking male baboons mate with females more often than low-ranking males, and rank is determined by fighting ability [46–49]. Therefore, immigrant males that rapidly attain a high rank in a new group simultaneously have the most to gain by killing fetuses and infants and are the most capable of carrying out successful attacks [21,22,50]. We predicted that the risk of feticide and infanticide would be higher after the immigration of such males. We also predicted that the males most likely to be feticidal or infanticidal would be those males that remain resident in a group after immigrating. It is not unusual for males in Amboseli to enter a group for a few days before leaving, only to return a few days later. This behaviour, here called 'shopping', might be repeated by a male several times before he becomes consistently resident in a group; occasionally, males that engage in extensive shopping never achieve consistent residency in a given group.

We compiled a list of first-time immigrations of males into a given study group between 1978 and 2015, drawing on our long-term census records. We divided these immigrations into two categories according to whether they represented males that we predicted would be more versus less likely to commit infanticide or feticide. We defined Category 1 immigrations ($N = 75$, 71 distinct males) as those in which an immigrant attained high rank (an ordinal dominance rank of 1, 2 or 3) within 90 days, did not shop before attaining high rank and remained in the group for at least 90 days after attaining high rank. By contrast, we defined as Category 2 ($N = 84$, 80 distinct males) immigrations as those in which males met at least one of the following criteria: (i) they failed to attain high rank within 90 days but did attain high rank within 180 days or (ii) they attained high rank within 90 days but also participated in shopping, and/or left the group within 90 days after the attainment of high rank. We excluded from consideration males that never attained high rank after immigrating. This is a conservative exclusion, because such males might have committed feticide or infanticide, although they had less to gain by doing so.

(c) Measuring the benefits and costs of feticide and infanticide

Males stand to benefit from feticide and infanticide if they mate with females that would not otherwise be sexually receptive. To confirm that presumed feticidal and infanticidal males gained reproductive benefits from their behaviours, we counted the number of mothers of dead fetuses or infants that mated with presumed feticidal and infanticidal males after the death of their infant or fetus. A potential cost of feticide and infanticide is the concurrent killing of the mother of the dead fetus or infant. We assessed whether killing females in the process of committing feticide or infanticide imposes prohibitive costs on males. We determined the median length of time that a Category 1 male maintained an ordinal rank of 1, 2 or 3 (how long he retained a reproductive advantage in the social group) and compared this tenure to the length of time that he would have to wait for the median pregnant female (three months pregnant) or median lactating female (infant age approx. six months) to resume cycling in the absence of a feticidal or infanticidal attack. The death of any female that would be expected to resume cycling before the end of a male's tenure in the absence of any feticidal or infanticidal behaviour constitutes the loss of reproductive opportunity.

(d) Testing for environmental contingency

To test whether environmental characteristics influence the likelihood of a male committing feticide and infanticide, we built a logistic regression model using the R function glm. We used an increase of two or more infant or fetal deaths following Category 1 immigration, relative to background deaths (measured as the number of deaths in the two weeks prior to immigrations) as the response variable. Our model included as predictors the number of infants and fetuses present in a group at the time of immigration, and whether an immigration occurred during a period of relatively low-resource availability. Four 'Category 1' immigrations involved males that also appeared in the dataset at a subsequent point in their life. In order to avoid pseudoreplication, only males' first immigrations ($N = 71$) were included in the model. This approach did not affect our results: including these males' second immigrations as independent immigrations had a negligible impact on model coefficients and p values.

(e) Data queries

All data were extracted from the long-term database of the Amboseli Baboon Research Project. Specifically, we extracted a list of immigrations that were then separated into Category 1 and Category 2 immigrations. We excluded immigrations that occurred during fission periods, because these periods have been linked to elevated infant death rates in other primates [51]. We then counted the number of infant and fetal deaths that occurred in the two-week period before and after each immigration event for both Category 1 and Category 2 immigrations. We also counted the total number of dependent infants (less than 1 year) and fetuses (pregnant females) that were present in a group for at least 1 day during the two weeks before and after immigrations and then calculated the rate at which those fetuses and infants died during the periods before and after male immigration. We repeated this procedure for 1- to 2-year-olds, who represent a control group, i.e. individuals that are vulnerable to aggressive males but having little-to-no nutritional dependence on the mother. We also queried the database to count sexual acts between feticidal or infanticidal males and mothers who had lost an infant or fetus following those males' immigrations. We also extracted the male tenure length at high rank (ordinal dominance ranks 1–3) for each Category 1 immigration, and the waiting time to cycling resumption for females that lost fetuses and infants after male immigrations.

By using a two-week time frame, we sought to prevent the overlap of multiple immigration time frames. We were able to isolate the effect of the immigration of a single Category 1 male in all cases except for one. Males KIM and SHO were two Category 1 males that immigrated into Alto's group on 18 February 1984. Prior to analysis, we decided that because the effects of their immigrations could not be isolated, we would treat the immigrations of KIM and SHO as a single unit. Deaths that occurred before and after their immigration were counted a single time, and they represented a single immigration in logistic regression analysis.
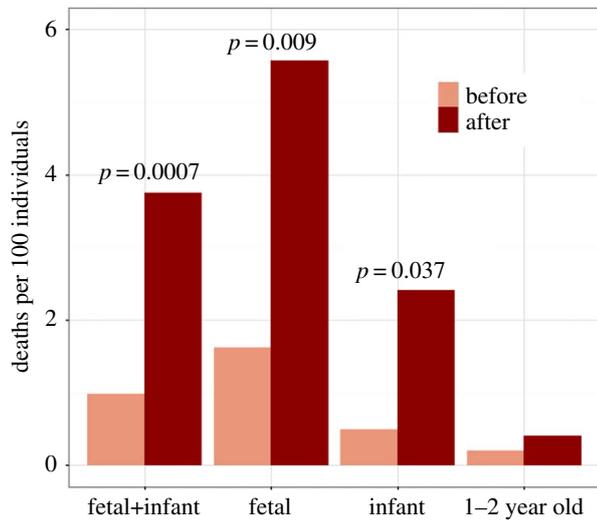
4

Figure 1. Changes in fetal and infant death rates following the immigration of Category 1 males. Statistically significant increases were seen in infant, fetal and combined infant and fetal death rates following the immigration of Category 1 males. No parallel increase was seen in death rates of 1- to 2-year-olds, indicating a lack of evidence for the hypothesis that elevated fetal and infant death rates were the result of generalized aggression. (Online version in colour.)

3. Results

(a) Presence of feticide and infanticide

Significantly more fetuses (Fisher's exact test, $p = 0.009$), infants ($p = 0.037$), and fetuses and infants combined ($p = 7 \times 10^{-4}$) died in the two weeks following Category 1 immigrations when compared with the two weeks prior to these immigrations, indicating that the period after a Category 1 immigration was a period of elevated risk for both fetuses and infants. No significant difference was found in the death rates of 1- to 2-year-olds following Category 1 immigrations ($p = 0.6$). We found no significant difference in the rates of fetal deaths ($p = 0.7$), infant deaths ($p = 0.8$), combined fetal and infant deaths ($p = 1$), or 1- to 2-year-old deaths ($p = 0.7$) following Category 2 immigrations when compared with the two weeks before Category 2 immigrations. These results are summarized in figure 1 and table 1.

(b) Cases of multiple deaths following immigrations

Most fetal and infant deaths following Category 1 immigrations were attributable to just seven of 75 Category 1 immigrations (no male was involved in more than one of these seven immigrations). Multiple fetal and infant deaths (range = $2-4$ were associated with each of these seven immigrations, totalling six infant and 13 fetal deaths. Both fetal and infant deaths occurred following five of these seven immigrations, while only fetal deaths occurred following two of these seven immigrations. Multiple infant and fetal deaths did not occur during the two-week period before any of the 75 Category 1 immigrations. The pattern of multiple deaths occurring within 14 days after, but never before, male immigration is consistent with two previously published case studies of apparent feticide in Amboseli [9,10]. In both of these studies, multiple females experienced fetal losses shortly after being attacked by particularly aggressive immigrant males. We obtained a conservative estimate of the frequency of fetal and infant deaths due to feticide and infanticide in this population

by counting only these cases of multiple deaths in our frequency estimation. This highly conservative estimate indicates that a minimum of 6.2% of fetal deaths (13/210) and 2.3% of infant deaths (6/258) that have occurred in the study groups are attributable to sexually selected feticide and infanticide.

(c) Ruling out environmental influences

In the two weeks following Category 1 immigrations, there was no significant change in fetal ($p = 0.2$), infant ($p = 0.8$), or combined fetal and infant ($p = 0.4$) death rates in the study groups other than the one into which males were immigrating as compared to the two weeks before immigration. During the two weeks following Category 1 immigrations, rates of fetal ($p = 2 \times 10^{-4}$), infant ($p = 0.005$) and combined fetal and infant ($p = 3 \times 10^{-6}$) death were significantly higher in the study groups into which males immigrated as compared to those groups into which males did not immigrate. During the two weeks prior to Category 1 immigrations, no significant differences in fetal ($p = 0.2$), infant ($p = 0.8$) or combined fetal and infant ($p = 0.6$) death rates existed between groups into which Category 1 males would soon immigrate and other study groups (electronic supplementary material, table S1).

(d) Testing the predictions of the sexual selection hypothesis

No extra-group paternity has ever been detected in more than 550 paternity assignments in this population, and none has ever been reported in other savannah baboon populations. Thus, a newly immigrated male is not the father of any infants or fetuses in the groups into which they immigrate. Fifteen females survived the death of their fetus or infant and all returned to cycling a median 41 days after fetal or infant death (interquartile range = 37.5–65 days). Thus, except in the case of infants whose mothers are nearing the end of post-partum amenorrhoea (population mean for live births = 323 days), infanticide would be expected to cause a female to return to cycling sooner than she otherwise would. Of the six presumed infanticides associated with these seven immigrations, none of the six females had begun cycling before the loss of their infant and four involved infants that were 31 days old or younger.

Of the surviving 15 females that lost a fetus or infant to presumed feticide or infanticide, 11 were mate-guarded by the immigrant male in question following the death of their fetus or infant. Seven of these mate-guarding episodes were observed before the female's next conception and five were observed within a week of the female's next conception, when conception probability is highest [52,53]. If these females had not lost their fetuses and infants, none would have been sexually receptive during the time of these conceptive mate-guarding episodes, so any mating with these females constitutes an increase in reproductive opportunities when compared with the reproductive environment that would have existed in the absence of fetal and infant death. The study animals are not under constant observation, and these results represent the most conservative estimate of the frequencies with which mothers that recently lost infants and fetuses mated with the male that caused their offspring's death.

Table 1. The number of fetuses and infants and fetal and infant deaths in the study groups into which Category 1 and 2 males immigrated.

immigration category	demographic category	deaths in two weeks before (N present)	deaths in two weeks after (N present)	Fisher's exact test, p-value
1 (N = 75)	fetuses	5 (308)	17 (305)	0.009
	infants	2 (408)	10 (415)	0.037
	fetuses + infants	7 (716)	27 (720)	0.0007
2 (N = 84)	fetuses	2 (368)	4 (372)	0.7
	infants	9 (571)	7 (571)	0.8
	infants + fetuses	11 (939)	11 (943)	1

(e) The costs of maternal deaths following male immigration

In our study, four of 19 mothers died along with their fetus or infant following the immigration of a presumed feticidal or infanticidal male, including three mothers on the same day. Three of these four females that died were lactating and one was pregnant. These deaths represent 80% (4/5) of all adult female deaths that occurred following Category 1 immigrations; i.e. aside from these four deaths, female death following immigrations was very rare.

The median length of time that Category 1 males spent at ranks 1, 2 or 3 following immigration was 12.5 months (interquartile range = 4.5–24), just longer than the average length of post-partum amenorrhoea in the population (mean = 323 days). For the median Category 1 male, the killing of a pregnant female along with her fetus does not impose a major immediate reproductive cost (electronic supplementary material, figure S2), as most males would not still be high ranking by the time that female would have resumed cycling in the absence of male interference (approx. 14 months after immigration for a female that is three months pregnant at the time of immigration). By contrast, the killing of the mother of a six-month-old infant constitutes a cost to the median Category 1 male, as that male would likely still be at high rank when that female would have resumed cycling (approx. six months after immigration) in the absence of male interference. Still, so long as maternal death remains an infrequent occurrence, the occasional loss of potential future reproductive opportunities is not enough to outweigh the benefits gained by feticidal and infanticidal males that successfully accelerate females' return to cycling.

(f) Contingent feticide and infanticide

We found that both feticide and infanticide were more common when more fetuses and infants were present in a group (coefficient = 0.54, p = 0.024) and when resource availability was relatively low (coefficient = 4.19, p = 0.016). Overall, the logistic regression model accounted for 52% of the variation in the presence of feticide and infanticide after the immigration of Category 1 males (electronic supplementary material, table S2). We also ran the model substituting the number of adults present in the group at the time of male immigration in place of the number of fetuses and infants. Although these two predictors are moderately correlated ($r^2 = 0.35$), the number of adults present in the group was not a significant predictor of the occurrence of presumed feticide and infanticide ($p > 0.05$).

4. Discussion

(a) Evidence for sexually selected feticide and infanticide

This study contributes two novel findings to our understanding of the conflict between pregnant and lactating females, whose preference is for their offspring to survive, and non-paternal males, whose preference is for females to be sexually receptive. First, our data indicate that sexually selected feticide exists in a wild population under the same conditions that favour the evolution of infanticide according to the sexual selection hypothesis. Specifically, we have shown that presumed feticidal and infanticidal males are unrelated to the individuals that die after their immigration, that females return to oestrous following presumed feticide and infanticide sooner than would otherwise be expected, and that females who have recently lost fetuses or infants often mate with presumed feticidal or infanticidal males. Our evidence does not support the hypothesis that fetal and infant deaths following male immigrations are the result of generalized male aggression towards all members of the population: rates of death among 1- to 2-year-old juveniles did not increase following male immigration. It is possible that immigrant males behave aggressively towards all females in a social group, and that this is one of the mechanisms involved in facilitating feticide and infanticide. We do not have adequately detailed behavioural observations over all decades of our study to make a strong test of this possibility, but it is not in accord with observations in chacma baboons, in which males have been observed to specifically target infants [16]. Second, we have shown that the likelihood of presumed feticide and/or infanticide occurring depends on characteristics of both the immigrant male and of his environment. Feticide and infanticide constitute contingent behavioural strategies that are employed by some males, at some times.

Strong evidence indicates that increases in fetal and infant death rates were not due to environmental causes. First, the use of a narrow temporal window for analysis (two weeks before and two weeks after each immigration) controls for all but the most acute environmental effects. The absence of seasonality in male immigrations, combined with the presence of increased fetal and infant death rates following Category 1 but not Category 2 immigrations provides further evidence that elevated death rates are linked to the immigration of particular males rather than environmental effects. Finally, if the environment were responsible for increases in fetal and infant death rates we would expect to see a parallel increase in fetal and infant death rates in the study groups into which males were not immigrating over the same time period.

No such increase was observed, and fetal and infant death rates were greater in groups into which males immigrated than those into which they did not immigrate.

(b) Feticide versus the Bruce effect

The rate of fetal death following Category 1 immigrations (17/305 pregnancies) is much lower than fetal death rates reported from studies of the Bruce effect [29,32,36,54], suggesting that fetal loss in our population is not an obligate response to male immigration. This finding, combined with previous case studies that document males physically attacking pregnant females [9,10], suggests that the increase in fetal death rate observed following the immigration of Category 1 males is the result of sexually selected feticide rather than a Bruce effect.

Bruce effects are believed to evolve in populations as a female counterstrategy against future infanticide. If it is highly likely that a female's offspring will be killed shortly after its birth, then natural selection favours a strategy in which she ceases to invest in a developing offspring [55]. Findings from this study suggest that sexually selected feticide might also drive the evolution of the Bruce effect. In populations where the risk of traumatic feticide is especially high, selection should favour the spontaneous abortion of pregnancies to prevent such aggression. A Bruce effect has likely failed to evolve in our population because of the relatively uncommon and unpredictable nature of feticidal and infanticidal behaviour. The majority of immigrant males in the study population are not feticidal or infanticidal, and on average the risk of fetal or infant loss following male immigration is low. Most of the time, then, Amboseli females can continue to invest energy in a pregnancy after the immigration of a new male without risking fetal or infant loss as a result of male behaviour. Hence, there is limited selective pressure in this population for females to terminate their pregnancies following the immigration of novel males.

(c) Feticide and infanticide as contingent male strategies

In several populations, infanticide has been described as a behavioural strategy that only some males employ [22–24], and our model provides some insight into the factors that create this contingency. Only Category 1 immigrations were associated with presumed feticide or infanticide, a finding that was consistent with expectations that high-quality males that became resident would be responsible for any male-induced increases in fetal and infant death in the population. Our logistic regression model demonstrated that presumed feticide and infanticide were also more likely to occur in groups that had a relatively large number of fetuses and infants present, which is consistent with a study in red howlers which found infanticide to be more likely to occur when more females were present in a group [56].

One third of Category 1 immigrations (6/18) that occurred during periods of low resource availability [39,43] were associated with multiple fetal and infant deaths. Two characteristics of low-resource periods may explain the increase in the frequency of presumed feticide and infanticide. First, during periods of low resource availability, inter-birth interval lengths were 15% longer on average [44]. This longer wait for females to become available following their offspring's birth would increase the pressure on males to commit feticide and infanticide. Second, during periods of low resource availability, social

groups' home ranges overlapped with the home ranges of relatively few other groups. Males typically disperse into social groups whose range overlaps with their own, and males are known to preferentially immigrate into groups with a relatively large number of available females [45,57]. However, this preference is more difficult to exercise when a dispersing male has fewer neighbouring social groups to choose between. In such circumstances, males are more likely to be forced to disperse into a group that contains relatively few available females. These males, in turn, may be more likely to employ feticide and infanticide in order to generate available females.

(d) Low frequency of infanticide in Amboseli

Although our estimate of the impact of presumed infanticide on infant mortality is very conservative, assessing only potential deaths that occurred within two weeks of male immigrations, the rate of infanticide in Amboseli (2.3% of infant mortality) appears to be much lower than that reported in the chacma baboons of Moremi. This assessment is based not only on the relatively low frequency of inferred feticide and infanticide reported here, but on the fact that infanticide by an immigrant male has only been directly observed twice in our population, which has been under observation since 1971. By contrast, infanticide by immigrant males in Moremi has been frequently documented and accounts for 29.4% [58] to 37% [22] of infant deaths (see electronic supplementary material, table S3).

This difference might be explained by the relative difference in benefits realized by males that kill infants in the two populations. In Moremi, the highest ranking male in a group reliably accounts for 78% of the total number of mate-guarding days during conceptive cycles and 45% of mate-guarding days during non-conceptive cycles [47]. By contrast, high-ranking males in Amboseli experience very high variance in the percentage of mate guarding they monopolize, with top-ranking males accounting for more than 80% of mate guarding during some periods, but less than 10% during other periods and only about 20% on average across the entire study [48]. Thus, being the highest ranking male in a group in Amboseli does not predict a male's ability to mate with a newly available female as well as it does in Moremi, reducing the relative benefits of feticide and infanticide in Amboseli relative to Moremi.

(e) Feticide versus infanticide from the male perspective

Presumed feticide has a greater impact on fetal death rates in our study population (accounting for at least 6.2% of all fetal deaths) than presumed infanticide on infant death rates (accounting for at least 2.3% of all infant deaths). This difference may reflect the greater difficulty of attacking and killing an infant than attacking a pregnant female [32]. Baboons have developed counter-strategies to infanticide, including the establishment of protective relationships with both paternal and non-paternal males [7]. In both yellow [59–61] and chacma [22,62–64] baboons, this protective relationship becomes dramatically stronger after birth, suggesting that males are more protective of infants than they are of fetuses. In addition, a male experiences a greater reduction in waiting time after committing feticide when compared with infanticide, as he is able to eliminate periods of both pregnancy and lactation (electronic supplementary material, figure S1), and this may also contribute to the higher rates of presumed feticide in Amboseli when compared with presumed infanticide. The

relative lack of protection afforded to fetuses, in combination with the relatively large potential benefits of inducing abortion as compared to killing infants, could make pregnant females the most attractive targets for immigrant males.

5. Conclusion

Many authors have argued that sexually selected infanticide results in selective pressures that have played an important role in the evolution of various social characteristics in primates (but see [65]), including male–female friendship [2], female coalitions [3], monogamy ([4,5], but see [66]) and social organization [6]. Yet sexually selected feticide, which should evolve under similar conditions as infanticide, receives relatively little attention in empirical studies or in discussions of the role of sexual conflict in social evolution. We argue that sexually selected feticide may have as strong an influence on the evolution of mammalian societies as does sexually selected infanticide. Given the relative difficulty of detecting fetal loss when compared with infant death, sexually selected feticide may occur, but remain undocumented, in many of the same populations in which infanticide has been observed. In these populations, sexually selected feticide can be seen as strengthening the selective pressures that result from sexually selected infanticide. It has been argued that feticide also occurs in populations where males are unable to kill infants, but are able to bring about fetal loss through male–female aggression [32]. In such populations, feticide in the absence of infanticide would represent a potentially important selective force that has not been previously considered.

References

1. Palombit RA. 2015 Infanticide as sexual conflict: coevolution of male strategies and female counterstrategies. *Cold Spring Harb. Perspect. Biol.* **7**, a017640. (doi:10.1101/cshperspect.a017640)

2. 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)

3. Treves A, Chapman CA. 1996 Conspecific threat, predation avoidance, and resource defense: implications for grouping in langurs. *Behav. Ecol. Sociobiol.* **39**, 43–53. (doi:10.1007/s002650050265)

4. Van Schaik CP, Dunbar RI. 1990 The evolution of monogamy in large primates: a new hypothesis and some crucial tests. *Behaviour* **115**, 30–61. (doi:10.1163/156853990×00284)

5. Opie C, Atkinson QD, Dunbar RI, Shultz S. 2013 Male infanticide leads to social monogamy in primates. *Proc. Natl Acad. Sci. USA* **110**, 13 328–13 332. (doi:10.1073/pnas.1307903110)

6. Pradhan GR, Van Schaik CP. 2008 Infanticide-driven intersexual conflict over matings in primates and its effects on social organization. *Behaviour* **145**, 251–275. (doi:10.1163/156853907783244710)

7. Smuts BB. 1985 *Sex and friendship in baboons*. Piscataway, NJ: Transaction Publishers.

8. Hrdy SB, Hausfater G. 1984 Comparitive and evolutionary perspectives on infanticide: introduction and overview. person *Infanticide: comparative and evolutionary perspectives* (eds SB Hrdy, G Hausfater), pp. pxiii–xxxv. New York, NY: Aldine Transaction.

9. Pereira ME. 1983 Abortion following the immigration of an adult male baboon (*Papio cynocephalus*). *Am. J. Primatol.* **4**, 93–98. (doi:10.1002/ajp.1350040109)

10. Alberts SC, Sapolsky RM, Altmann J. 1992 Behavioral, endocrine, and immunological correlates of immigration by an aggressive male into a natural primate group. *Horm. Behav.* **26**, 167–178. (doi:10.1016/0018-506x(92)90040-3)

11. Sommer V. 1987 Infanticide among free-ranging langurs (*Presbytis entellus*) at Jodhpur (Rajasthan/India): recent observations and a reconsideration of hypotheses. *Primates* **28**, 163–197. (doi:10.1007/bf02382569)

12. Sommer V. 1994 Infanticide among the langurs of Jodhpur: testing the sexual selection hypothesis with a long-term record. In *Infanticide and parental care* (eds S Parmigiani, FS Vom Saal), pp. 155–198. New York, NY: Routledge.

13. Agoramoorthy G, Mohnot SM, Sommer V, Srivastava A. 1988 Abortions in free ranging Hanuman langurs (*Presbytis entellus*)—a male induced strategy? *Hum. Evol.* **3**, 297–308. (doi:10.1007/bf02435859)

14. Hrdy SB. 1974 Male–male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatol.* **22**, 19–58. (doi:10.1159/000155616)

15. Hrdy SB. 1977 Infanticide as a primate reproductive strategy. *Am. Sci.* **65**, 40–49.

16. Palombit RA. 2003 Male infanticide in wild savanna baboons: adaptive significance and intraspecific variation. In *Sexual selection and reproductive competition in primates: new perspectives and directions* (eds CB Jones, OK Noman), pp. 367–412. Norman, OK: American Society of Primatologists.

17. Pusey AE, Packer C. 1994 Infanticide in lions: consequences and counterstrategies. In *Infanticide and parental care* (eds S Parmigiani, FS Vom Saal), pp. 277–299. New York, NY: Routledge.

18. Patterson IAP, Reid RJ, Wilson B, Grellier K, Ross HM, Thompson PM. 1998 Evidence for infanticide in bottlenose dolphins: an explanation for violent interactions with harbour porpoises? *Proc. R. Soc. Lond. B* **265**, 1167–1170. (doi:10.1098/rspb.1998.0414)

19. Dunn DG, Barco SG, Pabst DA, McLellan WA. 2010 Evidence for infanticide in bottlenose dolphins of the Western North Atlantic. *J. Wildl. Dis.* **38**, 505–510. (doi:10.7589/0090-3558-38.3.505)

20. Solomon NG, Keane B. 2007 Reproductive strategies in female rodents. In *Rodent societies: an ecological and evolutionary perspective* (eds JO Wolff, P Shermann), pp. 42–56. Chicago, IL: University of Chicago Press.

21. Teichroeb JA, Sicotte P. 2008 Infanticide in ursine colobus monkeys (*Colobus vellerosus*) in Ghana: new

8

cases and a test of the existing hypotheses. *Behaviour* **145**, 727–755. (doi:10.1163/156853908783929160)

22. Palombit RA, Cheney JF. 2000 Male infanticide and defense in chacma baboons. In *Infanticide by males and its implications* (eds CP Van Schaik, CH Janson), pp. 123–151. Cambridge, MA: Cambridge University Press.

23. Cords M, Fuller JL. 2010 Infanticide in *Cercopithecus mitis stuhlmanni* in the Kakamega Forest, Kenya: variation in the occurrence of an adaptive behavior. *Int. J. Primatol.* **31**, 409–431. (doi:10.1007/s10764-010-9400-z)

24. Sommer V. 2000 The holy wars about infanticide. Which side are you on? and why? In *Infanticide by males and its implications* (eds CP Van Schaik, C Janson), pp. 9–26. Cambridge, UK: Cambridge University Press.

25. Bruce HM. 1959 An exteroceptive block to pregnancy in the mouse. *Nature* **184**, 105. (doi:10.1038/184105a0)

26. Bruce HM. 1960 A block to pregnancy in the mouse caused by proximity of strange males. *J. Reprod. Fertil.* **1**, 96–103. (doi:10.1530/jrf.0.0010096)

27. Labov JB. 1981 Pregnancy blocking in rodents: adaptive advantages for females. *Am. Nat.* **118**, 361–371. (doi:10.1086/283828)

28. Bertram BC. 1975 Social factors influencing reproduction in wild lions. *J. Zool. (Lond.)* **177**, 463–482. (doi:10.1111/j.1469-7998.1975.tb02246.x)

29. Roberts EK, Lu A, Bergman TJ, Beehner JC. 2012 A Bruce effect in wild geladas. *Science* **335**, 1222–1225. (doi:10.1126/science.1213600)

30. Bartoš L, Bartošová J, Pluháček J, Šindelářová J. 2011 Promiscuous behaviour disrupts pregnancy block in domestic horse mares. *Behav. Ecol. Sociobiol.* **65**, 1567–1572. (doi:10.1111/j.1469-7998.1975.tb02246.x)

31. Pluháček J, Bartoš L. 2005 Further evidence for male infanticide and feticide in captive plains zebra, *Equus burchelli*. *Folia Zool.* **54**, 258–262. (doi:10.1006/anbe.1999.1371)

32. Berger J. 1983 Induced abortion and social factors in wild horses. *Nature* **303**, 59–61. (doi:10.1038/303059a0)

33. Bruce HM, Parkes AS. 1960 Hormonal factors in exteroceptive block to pregnancy in mice. *J. Endocrinol.* **20**, pxxix–xxx.

34. Parkes AS, Bruce HM. 1961 Olfactory stimuli in mammalian reproduction: odor excites neurohumoral responses affecting oestrus, pseudopregnancy, and pregnancy in the mouse. *Science* **134**, 1049–1054. (doi:10.1126/science.134.3485.1049)

35. Milligan SR. 1976 Pregnancy blocking in the vole, *Microtus agrestis*. *J. Reprod. Fertil.* **46**, 97–100. (doi:10.1530/jrf.0.0460091)

36. Fraser-Smith AC. 1975 Male-induced pregnancy termination in the prairie vole, *Microtus ochrogaster*. *Science* **187**, 1211–1213. (doi:10.1126/science.1114340)

37. Pearlman MD, Tintinalli JE, Lorenz RP. 1990 Blunt trauma during pregnancy. *N. Engl. J. Med.* **323**, 1609–1613. (doi:10.1056/nejm199012063232307)

38. Alberts SC, Altmann J. 2012 In *Long-term field studies of primates* (eds PM Kappeler, DP Watts), pp. 261–287. New York, NY: Springer.

39. Alberts SC, Hollister-Smith JA, Mututua RS, Sayialel SN, Muruthi PM, Warutere JK, Altmann J. 2005 Seasonality and long term change in a savannah environment. In *Seasonality in primates: studies of living and extinct human and non-human primates* (eds DK Brockman, CP Van Schaik), pp. 157–196. Cambridge, MA: Cambridge University Press.

40. Beehner JC, Nguyen N, Wango EO, Alberts SC, Altmann J. 2006 The endocrinology of pregnancy and fetal loss in wild baboons. *Horm. Behav.* **49**, 688–699. (doi:10.1016/j.yhbeh.2005.12.016)

41. Altmann SA. 1970 The pregnancy sign in savannah baboons. *Lab. Anim. Dig.* **6**, 7–10.

42. Hausfater G. 1975 Dominance and reproduction in Baboons (*Papio cynocephalus*). *Contrib. Primatol.* **7**, 1–150.

43. Bronikowski AM, Altmann J. 1996 Foraging in a variable environment: weather patterns and the behavioral ecology of baboons. *Behav. Ecol.* **39**, 11–25. (doi:10.1007/s002650050262)

44. Altmann J, Alberts SC. 2003 Variability in reproductive success viewed from a life-history perspective in baboons. *Am. J. Hum. Biol.* **15**, 401–409. (doi:10.1002/ajhb.10157)

45. Alberts SC, Altmann J. 1995 Balancing costs and opportunities: dispersal in male baboons. *Am. Nat.* **145**, 279–306. (doi:10.1086/285740)

46. Packer C. 1985 Dispersal and inbreeding avoidance. *Anim. Behav.* **33**, 676–678. (doi:10.1016/s0003-3472(85)80096-8)

47. Bulger JB. 1993 Dominance rank and access to estrous females in male savanna baboons. *Behaviour* **127**, 67–103. (doi:10.1163/156853993×00434)

48. Alberts SC, Watts HE, Altmann J. 2003 Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. *Anim. Behav.* **65**, 821–840. (doi:10.1006/anbe.2003.2106)

49. Strum SC. 1982 Agonistic dominance in male baboons: an alternative view. *Int. J. Primatol.* **3**, 175–202. (doi:10.1007/bf02693494)

50. Soltis J, Thomsen R, Matsubayash K, Takenaka O. 2000 Infanticide by resident males and female counter-strategies in wild Japanese macaques (*Macaca fuscata*). *Behav. Ecol. Sociobiol.* **48**, 195–202. (doi:10.1007/s002650000224)

51. Ménard N, Vallet D. 1993 Dynamics of fission in a wild Barbary macaque group (*Macaca sylvanus*). *Int. J. Primatol.* **14**, 479–500. (doi:10.1007/bf02192778)

52. Shaik AA, Celaya CL. 1982 Temporal relationship of hormonal peaks to ovulation and sex skin deturgescence in the baboon. *Primates* **3**, 444–452. (doi:10.1007/bf02381326)

53. Wildt DE, Doyle LL, Stone SC, Harrison RM. 1977 Correlation of perineal swelling with serum ovarian hormone levels, vaginal cytology, and ovarian follicular development during the baboon reproductive cycle. *Primates* **18**, 261–270. (doi:10.1007/bf02383104)

54. Hackländer K, Arnold W. 1999 Male-caused failure of female reproduction and its adaptive value in alpine marmots (*Marmota marmota*). *Behav. Ecol.* **10**, 592–597. (doi:10.1093/beheco/10.5.592)

55. Pillay NA, Kinahan AA. 2009 Mating strategy predicts the occurrence of the Bruce effect in the vlei rat *Otomys irroratus*. *Behaviour* **146**, 139–151. (doi:10.1163/156853908×390968)

56. Crockett CM, Janson CH. 2000 Infanticide in red howlers: female group size, male membership, and a link to folivory. In *Infanticide by males and its implications* (eds CP Van Schaik, CH Janson), pp. 75–98. Cambridge, MA: Cambridge University Press.

57. Altmann J. 2000 Predicting male distribution among primate groups. In *Primate males: causes and consequences of variation in group composition* (ed. PM Kappeler), pp. 236–247. Cambridge, MA: Cambridge University Press.

58. Collins DA, Busse CD, Goodall J. 1984 Infanticide in two populations of savanna baboons. In *Infanticide: comparative and evolutionary perspectives* (eds SB Hrdy, G Hausfater), pp. 193–215. New York, NY: Aldine Transaction.

59. Altmann J. 1980 *Baboon mothers and infants*. Cambridge, MA: Harvard Univ. Press.

60. Stein DM. 1984 *The sociobiology of infant and adult male baboons*. New York, NY: Ablex Publishing Corp.

61. 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. (doi:10.1007/s00265-009-0786-6)

62. Palombit RA, Seyfarth RM, Cheney DL. 1997 The adaptive value of 'friendships' to female baboons: experimental and observational evidence. *Anim. Behav.* **54**, 599–614. (doi:10.1006/anbe.1996.0457)

63. Palombit RA, Cheney DL, Seyfarth RM. 2001 Female–female competition for male 'friends' in wild chacma baboons (*Papio cynocephalus ursinus*). *Anim. Behav.* **61**, 1159–1171. (doi:10.1006/anbe.2000.1690)

64. Moscovice LR, Di Fiore A, Crockford C, Kitchen DM, Wittig R, Seyfarth RM, Cheney DL. 2010 Hedging their bets? Male and female chacma baboons form friendships based on likelihood of paternity. *Anim. Behav.* **79**, 1007–1015. (doi:10.1016/j.anbehav.2010.01.013)

65. Lukas D, Huchard E. 2014 The evolution of infanticide by males in mammalian societies. *Science* **346**, 841–844. (doi:10.1126/science.1257226)

66. Lukas D, Clutton-Brock TH. 2013 The evolution of social monogamy in mammals. *Science* **341**, 526–530. (doi:10.1126/science.1238677)

67. Zipple MN, Grady JH, Gordon JB, Chow LD, Archie AE, Altmann J, Alberts SC. 2017 Data from: Conditional fetal and infant killing by male baboons. Dryad Digital Repository. (http://datadryad.org/resource/doi:10.5061/dryad.c4b89)