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When will the Bruce effect evolve? The roles of infanticide, feticide and maternal death

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In many mammalian species, males are selected to kill unrelated infants and/or fetuses in order to cause lactating and pregnant females to begin cycling sooner than they otherwise would. As a result, females have evolved numerous counterstrategies to prevent infanticide and feticide. One such proposed counterstrategy is the Bruce effect, an apparently costly strategy in which inseminated or pregnant females cease reproductive investment in a developing embryo or fetus following exposure to nonsire males. Here I present a quantitative model that seeks to explain under what conditions females will be selected to exhibit the Bruce effect (i.e. to block or terminate pregnancy) rather than risking future infanticide or feticide. I first present an analytical model of the costs of the Bruce effect relative to the costs of potential feticide or infanticide. I then test the resulting predictions using an individual-based model operating under ecologically relevant conditions. The individual-based model predicts that moderate and high, but not low, levels of infanticide can produce selection for the Bruce effect. In contrast, feticide risk alone is unlikely to lead to selection for the Bruce effect, although feticide risk coupled with a substantial risk of female mortality following feticidal attack can. The model correctly predicts the evolution of the Bruce effect in geladas, *Theropithecus gelada,* and correctly predicts the absence of a Bruce effect in chacma baboons, *Papio ursinus*, and yellow baboons, *Papio cynocephalus*. Finally, I present a framework by which researchers can predict whether they expect to find infanticide, feticide and/or the Bruce effect in their study species.

Nonsire males benefit from infanticide by killing the infants of lactating females, thereby causing the females to return to fertility sooner than they would if the females had instead weaned their infant before becoming fertile (Hausfater & Hrdy, 1984; Hrdy, 1974; van Schaik, 2009). These benefits to males generally only occur along a relatively narrow range of the mammalian taxonomy in which species reproduce nonseasonally and the length of lactation exceeds the length of gestation (i.e. species that display postpartum amenorrhea) (Palombit, 2015; van Schaik, 2000). Despite this narrow range, infanticide by males and its purported counterstrategies by females have received a huge amount of empirical and theoretical attention in behavioural ecology and evolutionary biology (Palombit, 2015).

Feticide by males is a related form of sexual conflict in which males attack pregnant females and thereby induce pregnancy termination (Agoramoorthy, Mohnot, Sommer, & Srivastava, 1988; Alberts, Sapolsky, & Altmann, 1992; Pereira, 1983; Sommer, 1994; Zipple et al., 2017). Feticide might confer reproductive benefits to males across a much wider range of the mammalian taxonomy than does infanticide by males. Indeed, because there are not species in which a pregnant female can become pregnant again by a nonsire male, nonsire males of nearly all mammalian species may benefit from killing the embryos or fetuses of inseminated or pregnant females (Zipple, Roberts, Alberts, & Beehner, 2019). Yet, the theoretical and empirical literature regarding feticide and its counterstrategies are relatively unexplored, most likely due to the difficulty of identifying fetal loss in wild populations.

Females are not passive participants in sexual conflict and have instead evolved numerous counterstrategies to infanticide (and possibly also to feticide) (Palombit, 2015). One proposed counterstrategy to infanticide and feticide is the Bruce effect, a phenomenon by which females terminate existing reproductive investment, either through blocking of implantation or through pregnancy termination, following nontraumatic exposure to nonsire males (Bartoš et al., 2011, 2016; Bronson & Eleftheriou, 1963; Bruce, 1959; Kenney, Evans, & Dewsbury, 1977; Roberts, Lu, Bergman, & Beehner, 2012; Stehn & Richmond, 1975). The Bruce effect is

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distinct from feticide, as the Bruce effect does not necessarily involve any aggression from males and is likely to affect all or nearly all pregnant females in a social group. Feticide necessarily involves aggression from males to pregnant females and is likely to affect only a subset of pregnant females targeted by nonsire males (Zipple et al., 2019).

Verbal models have long argued that by terminating investment in offspring that are likely to be future victims of infanticide, females can reduce the costs of infanticidal behaviour following male take-over (Labov, 1981; Schwagmeyer, 1979). These verbal models were recently expanded to include feticide avoidance as an additional or alternative benefit of the Bruce effect for females (Zipple et al., 2019). Although useful, these verbal models are limited in their predictive scope. For example, it seems incontrovertible that the cost to a female of terminating a pregnancy following male take-over is lower than maintaining the pregnancy if she is certain to later lose the offspring as a result of a feticidal or infanticidal attack. Yet, in many systems, exposure to a nonsire male does not necessarily predict future infanticidal loss, as infanticide risk varies depending on characteristics of the male, the female and their environment (Bartoš et al., 2011, 2016; Cheney et al., 2004; Crockett & Janson, 2000; Eccard, Dammhahn, & Ylönen, 2017; Storey & Snow, 1990; Zipple et al., 2017). Thus, the extent to which the Bruce effect can serve as a cost-mitigating strategy may be critically dependent on the likelihood of future infanticide or feticide in the absence of pregnancy block or termination.

Here I quantify the costs and benefits associated with the Bruce effect as a counterstrategy to feticide and/or infanticide for female mammals. I first provide an analytical model of the costs and benefits of the Bruce effect in this context and then test this analytical model by simulating lifetime reproductive success of females under ecologically relevant conditions. This individual-based model allows me to consider the roles of male take-over frequency and the physical costs of infanticide and feticide in the calculation of the net benefits or costs realized by females that exhibit the Bruce effect. These models serve as a test of the hypothesis that the Bruce effect could evolve as a counterstrategy to feticide and/or infanticide. Although the models assume a life history that most closely mirrors that of primates, these results yield predictions that can be applied to a variety of mammalian life histories.

METHODS

Analytical Model

The goal of the analytical model is to quantify the expected costs to pregnant and lactating females presented by male take-over due to potential feticide and infanticide. Throughout, take-overs are assumed to involve males that have not mated previously with any females in the group (i.e. they are definitely not the father of any fetuses or infants in the group). The modelled females give birth to a single offspring, must wean their current offspring before they conceive again, and encounter periodic male take-over events that entail varying risks of fetal or infant death. I first assume that a female achieves the highest fitness by producing as many surviving offspring as possible during her lifetime, and that the number of offspring she can produce is limited by her reproductive life span. The analytical model therefore considers only the temporal costs of feticide, infanticide and the Bruce effect. Other costs of infanticide and/or feticide may exist, including increased physical and social stress, an issue that I partially address later when building an individual-based model.

I assume that male take-overs occur and that among pregnant females, the gestational age of pregnancies is uniformly distributed at the time of take-over. This assumption allows me to treat the average pregnant female as being at the half-way point of her pregnancy at the time of a male take-over. I designate gestation time as G, so the average pregnant female has invested $G/2$ units of time into her pregnancy when the male take-over occurs. In this model, time is measured in months, but to adapt the model to animals with shorter or longer life spans, units could be changed to any length of time. Next, I assume that either a recurrent risk of feticide, p_{fet}, occurs each month following male take-over until the female gives birth, or a recurrent risk of infanticide, p_{inf}, occurs each month from birth until the age at weaning, L. In both the analytical and individual-based models, infanticide risk and feticide risk are mutually exclusive, although they need not be in a real population.

The expected temporal cost of potential feticide is the sum of the expected cost each month following male take-over. In the first month following male take-over this expected cost is the investment up to that point ($G/2$) times the risk of feticide (p_{fet}):

$$\left(\frac{G}{2}\right)\left(p_{\text{fet}}\right) \tag{1}$$

In each successive month, females face an additional risk of feticide, conditional on feticide having not previously occurred. Summing across all months following take-over until birth (expected to be $G/2$ months) yields the total expected cost of feticide risk for a pregnant female following a male take-over (investment $\times$ risk of feticide $\times$ probability feticide has not previously occurred):

$$\sum_{n=1}^{\frac{G}{2}}\left(\frac{G}{2}+n-1\right)\left(p_{\text{fet}}\right)\left(1-p_{\text{fet}}\right)^{n-1} \tag{2}$$

The expected cost of infanticide risk (p_{inf}) for pregnant females begins to accrue after the offspring is born. In the offspring's first month of life, the expected cost of infanticide risk in terms of maternal time investment is investment $\times$ risk of infanticide:

$$(G)\left(p_{\text{inf}}\right) \tag{3}$$

And the total expected cost of infanticide risk across all months prior to weaning is (investment $\times$ risk of infanticide $\times$ probability infanticide has not previously occurred):

$$\sum_{n=1}^{L}(G+n-1)\left(p_{\text{inf}}\right)\left(1-p_{\text{inf}}\right)^{n-1} \tag{4}$$

If a female exhibits the Bruce effect and terminates pregnancy immediately following male take-over, the expected cost of this strategy is simply the time invested in reproduction up to this point, which is on average $G/2$.

For the Bruce effect to be selected for in response to feticide or infanticide, the costs of the Bruce effect must be lower than the future costs of feticide or infanticide. To explore the parameter space where this is true, I held L constant at 12 months and varied G from 4 to 18 months (representing between-species variation in the L/G ratio). I then allowed p_{inf} and p_{fet} to vary from 0 to 1 in increments of 0.01 and calculated the costs of feticide or infanticide relative to the costs of the Bruce effect ($G/2$).

Individual-based Model

The above analytical model considers the net benefits of the Bruce effect during a single pregnancy. The analytical model is not iterative and as a result does not predict whether the Bruce effect is beneficial to females across their entire life span and across

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Table 1
Parameters used in the analytical model of the costs of the Bruce effect relative to the costs of potential feticide or infanticide and an individual-based model (IBM) operating under ecologically relevant conditions

Parameter	Appears in	Description
G	Both models	Gestation length for a female (in IBM 6, 12, or 18 months)
L	Both models	Lactation length (12 months)
p_{fet}[a]	Both models	Monthly probability of feticidal attack following male take-over (in IBM $0 \leq p_{fet} \leq 0.2$)
p_{inf}[a]	Both models	Monthly probability of infanticidal attack following male take-over (in IBM $0 \leq p_{inf} \leq 0.2$)
p_{take}[a]	IBM only	Monthly probability of a male take-over ($0 \leq p_{take} \leq 0.3$)
p_{death}[a]	IBM only	Risk of maternal death as a result of feticidal or infanticidal attack (in IBM $0 \leq p_{death} \leq 0.25$)
Age_max	IBM only	The maximum age for a female (drawn from N (18,4))
Strategy	IBM only	Binary; either 'Bruce' or 'maintain'. Pregnant females exhibiting the Bruce strategy terminate pregnancies immediately after male take-over. The Bruce strategy reduces p_{death} to zero

[a] Ranges of parameters were chosen to encompass the range of parameters most likely to occur in nature.

multiple male take-overs. To evaluate the analytical model under ecologically relevant conditions, I built an individual-based model of female mammals living in the same life history context as the analytical model: they give birth to a single offspring, they must wean their current offspring before they conceive again, and they may experience a risk of feticide or infanticide following male take-over. I asked whether females in this context derive a fitness benefit from terminating pregnancies following male take-over. The modelled females are relatively long-lived (maximum life span is normally distributed around 18 years), but this approach should be generalizable to any mammal species for whom life span and reproductive cycle lengths are known. All parameters described below were randomly assigned at birth and held constant during a female's life. Descriptors of parameters included in the individual-based model as well as the range of values explored for each parameter are included in Table 1. The processes involved in the individual-based model (IBM) are visually summarized in Fig. 1.

Beginning at 6 years of age, all females experienced repeated interbirth intervals until they reached a maximum age (age_max), which was drawn from a normal distribution with mean 18 years and standard deviation of 2 years for each female. All interbirth intervals began with 4 months of cycling, followed by some months of pregnancy (G), and then followed by 12 months of lactation (L). For each month of a female's life, whether a male take-over occurred was drawn from a binomial distribution where the probability of male take-over in a given month was p_{take}, which I allowed to vary from 0 to 0.3. Females' lives continued until they reached their age_max, at which point they died and I counted the total number of offspring they had that had already reached 12 months of age.

Each female experienced either a risk of feticide or infanticide following male take-over. For a female at risk of feticide, if she experienced male take-over during pregnancy, she then faced a risk of experiencing feticide, p_{fet}, during the month in which the take-over occurred and each month thereafter. If a female at risk of infanticide experienced male take-over during pregnancy, her offspring faced a risk of infanticide each month p_{inf} from its birth until the end of lactation at 12 months. Any female that lost her fetus or infant to feticide or infanticide faced an additional risk of death as a result of male aggression associated with feticidal or infanticidal attack, p_{death}. Females that experienced feticidal or infanticidal loss and survived restarted their interbirth interval cycle and became pregnant again after 4 months.

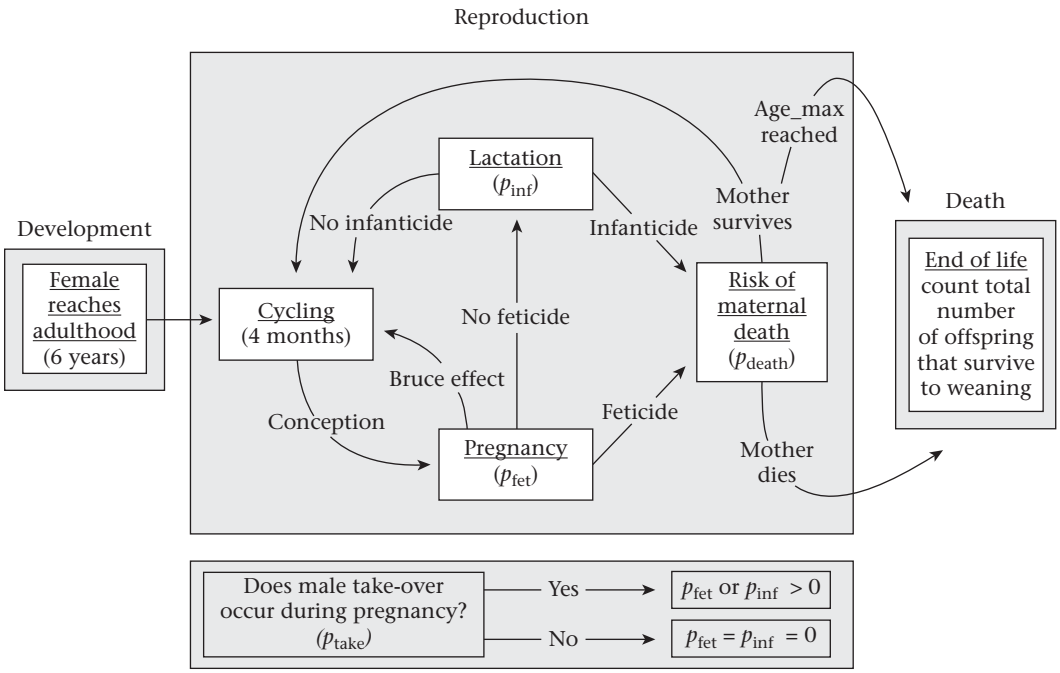

Figure 1. The processes involved in the individual-based model. All parameters are randomly assigned at a female's birth and are held constant throughout her lifetime.

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Half of the females exhibited the Bruce effect as a life history strategy. In these cases, females who were pregnant at the time of male take-over immediately terminated their pregnancy and reset their interbirth interval. Females who reset themselves did not face a risk of death as a result of male aggression ($p_{death} = 0$).

For each set of parameters, I calculated the average lifetime reproductive success for all females that made use of the Bruce effect and compared this to the average lifetime reproductive success for females that did not make use of the Bruce effect.

RESULTS

Analytical Model

The analytical model yields two main results, which are displayed in Fig. 2. First, the analytical model indicates that, regardless of gestation length, both risk of feticide and infanticide can result in scenarios where the Bruce effect yields net reproductive benefits to pregnant females. Second, the benefits derived from the Bruce effect as a method of feticide avoidance are rather small (less than 2 months gained at all gestation lengths from 4 to 18 months) compared to the interbirth interval of the modelled animal (at least 16–30 months based on the values of L and G) and these benefits begin to accrue only when monthly risk of feticide is high ($p_{fet} > 0.15$ when $G = 18$ months) or extremely high ($p_{fet} > 0.67$ when $G = 4$). In contrast, the benefits of the Bruce effect derived from infanticide avoidance were higher at their peaks (4.6–11 months depending on G) and the Bruce effect began to deliver some benefits even when monthly infanticide risk remained relatively low ($p_{inf} > 0.03$–0.05, depending on G). The results of the analytical model suggest that infanticide avoidance, but not feticide avoidance, is likely to lead to lifetime benefits for females under ecologically relevant conditions.

Individual-based Model

Termination of pregnancy always represents an absolute cost to females. The question of interest in this individual-based model is whether pregnancy termination confers benefits relative to pregnancy maintenance if pregnancy maintenance increases the risk of future costs of feticide or infanticide.

The absolute costs of pregnancy termination experienced by females in the individual-based model are equal to the average difference in reproductive success between 'maintain' and Bruce effect strategies when there is no risk of feticide or infanticide ($p_{fet} = p_{inf} = 0$). These costs are well predicted by two factors: length of gestation, G, and the monthly probability of male take-over, p_{take} (Fig. 3). When gestation length is longer, the amount of reproductive investment that females sacrifice by terminating pregnancies is greater. When male take-over is more common, the frequency with which that sacrifice is made is higher. The remainder of the results discussed here assume a gestation length of 6 months. Varying gestation length does not qualitatively change the results (Supplementary material 1, Fig. S1).

Risk of feticide and/or infanticide both increased the net benefits of the Bruce effect following male take-over, but their effects were not equal. High levels of infanticide were generally sufficient for the Bruce effect to yield net benefits to females in the absence of any risk of maternal death following infanticide. In contrast, in the absence of infanticide, high levels of feticide were necessary for the Bruce effect to deliver net benefits to females, but they were not sufficient in the absence of substantial risk of maternal death following feticide (Fig. 4).

Increasing the frequency of male take-over creates ever higher absolute costs of the Bruce effect. So long as male take-over remains a relatively uncommon event, a high enough probability of infanticide or a high enough probability of feticide coupled with risk of maternal death can always create conditions under which females derive a net benefit from the Bruce effect. However, if male take-over is frequent enough, then the costs of termination every time there is a male take-over can never be overcome, regardless of how likely feticide or infanticide may be. Indeed, when male take-over is very common (monthly probability of take-over $\geq$0.15), the Bruce effect almost always yields net costs for females (Fig. 5).

DISCUSSION

The results of the analytical and individual-based models demonstrate a wide range of conditions under which the Bruce

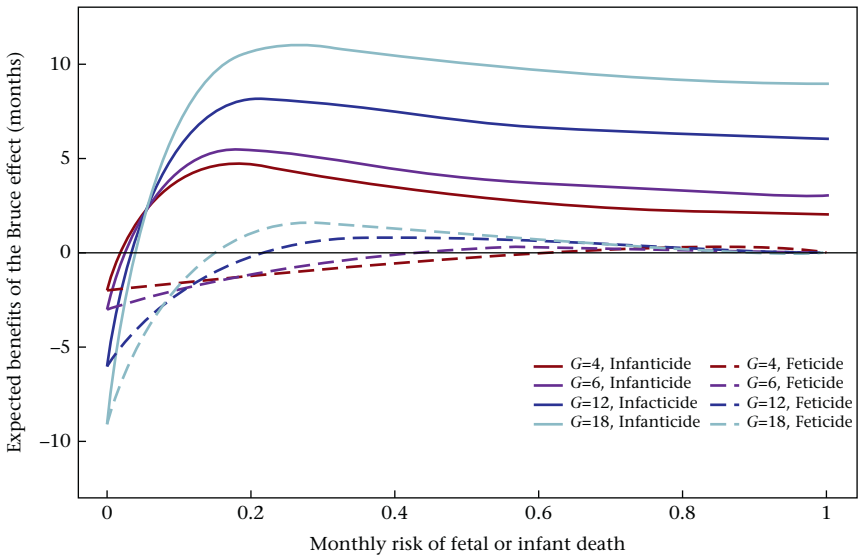

Figure 2. Results from the analytical model. The Bruce effect provides benefits to pregnant females when risks of infanticide or feticide are high enough. Although a low risk of infanticide (monthly $p_{inf} \approx 0.03$–0.05) can lead to net benefits from the Bruce effect, feticide must occur at a higher rate in order for females to benefit from the Bruce effect and these benefits are much reduced when they do occur. Solid lines indicate benefits derived from infanticide avoidance while dashed lines indicate benefits derived from feticide avoidance.

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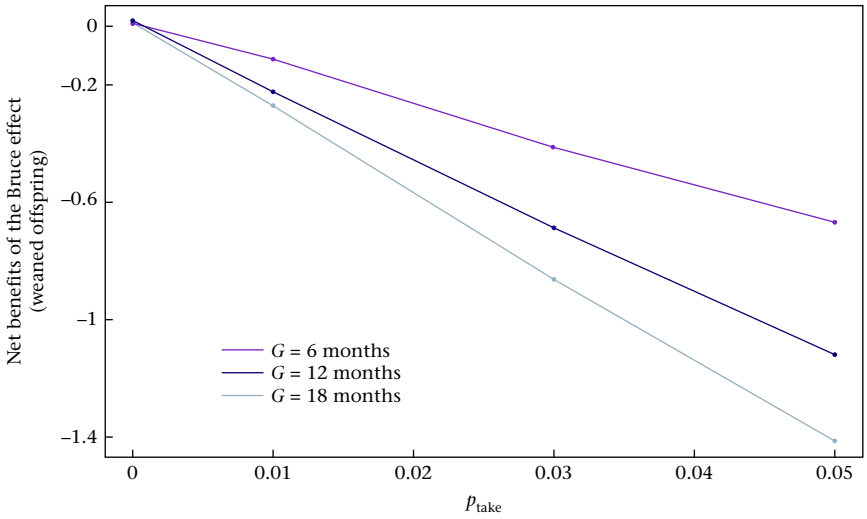

Figure 3. Costs of the Bruce effect in the individual-based model increase as a function of gestation length and likelihood of male take-over. More negative values correspond to higher costs.

effect can be beneficial for pregnant females. Under these conditions, the costs of pregnancy termination following male take-over can be readily balanced by avoiding future costs of infanticide when risk of infanticide is moderate or high. Avoiding the future costs of feticide does not produce a comparable balance, because the expected temporal costs of feticide are lower than the expected costs of infanticide. However, if a substantial probability (0.25) of maternal death accompanies a feticidal attack, then feticide avoidance can also result in the Bruce effect yielding net benefits to females.

The results of the analytical and individual-based models are qualitatively consistent, but the analytical model generally predicts that benefits of pregnancy termination will begin at lower levels of monthly infanticide risk than does the individual-based model. While the analytical model predicts benefits from the Bruce effect when monthly probability of infanticide is in the 0.05–0.10 range, the individual-based model does not generally predict lifetime

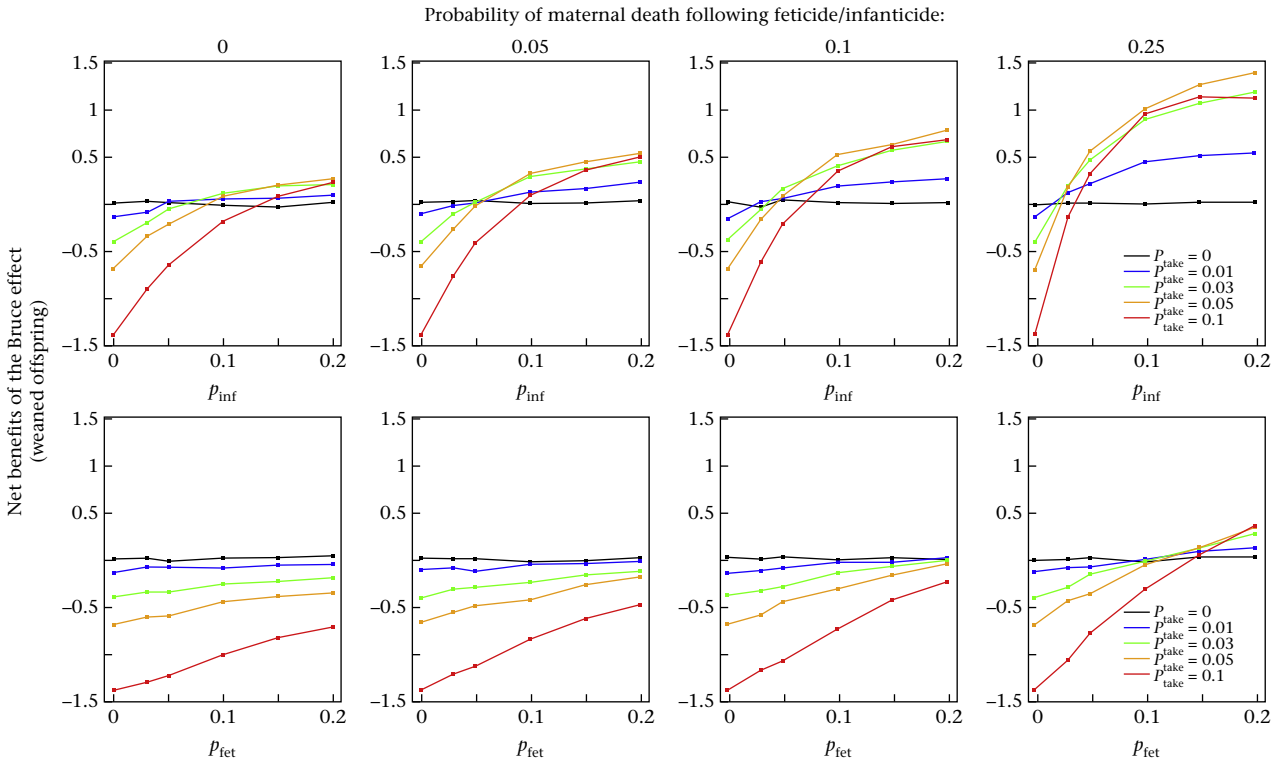

Figure 4. Results from the individual-based model. The top row of plots shows the net reproductive benefits of the Bruce effect for females as risk of infanticide following take-over and frequency of take-over are allowed to change (risk of feticide is held constant at zero). The bottom row shows the net reproductive benefits of the Bruce effect for females as risk of feticide following take-over is allowed to change (risk of infanticide is held constant at zero). Positive values reflect regions of the parameter space where the Bruce effect is expected to be selected for. Noise around the black line ($p_{take} = 0$) reflects variation in reproductive success as a result of introduced variation in life span.

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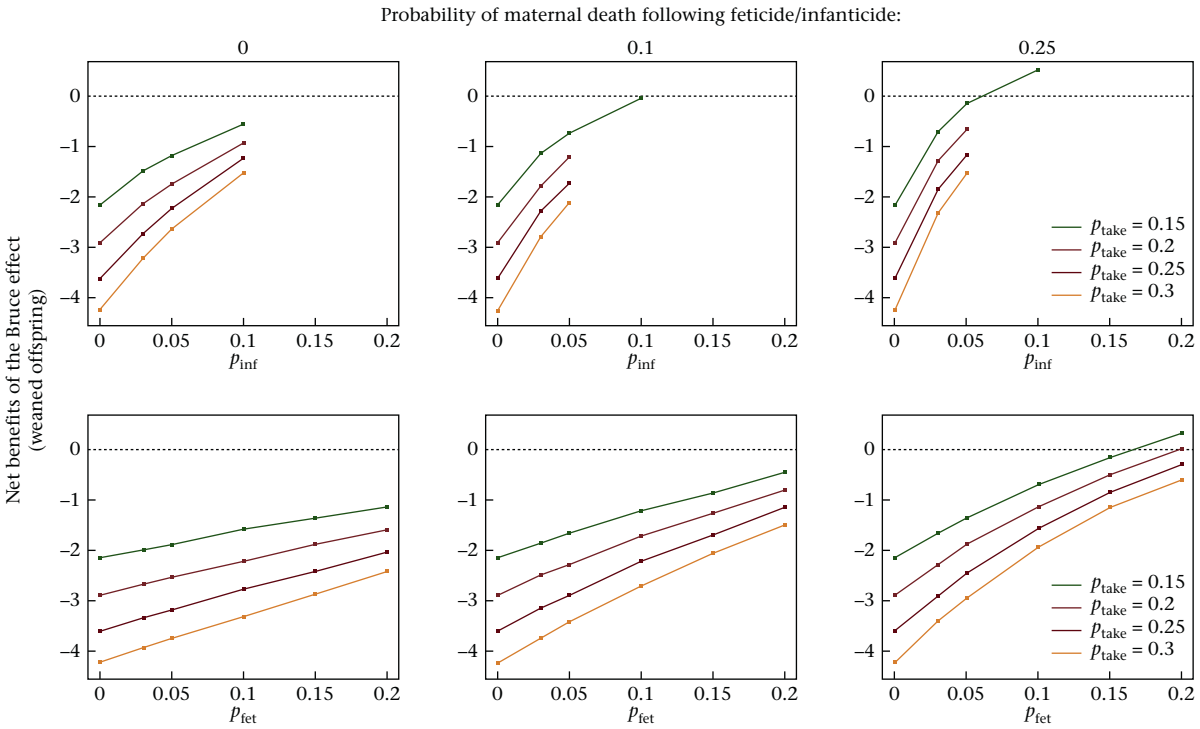

Figure 5. Individual-based model results when male take-over is common. As the frequency of male take-over increases to very high levels, the parameter space for which the Bruce effect is beneficial for females (i.e. when net benefits are greater than zero) nearly disappears. This increase in male take-over frequency can be thought of as a reduction in the ratio of interbirth interval to male tenure length. As in Fig. 4, the top row of plots shows outcomes of the individual-based model when infanticide risk is nonzero and feticide risk is held constant at zero, while the bottom row reflects outcomes when feticide risk is nonzero and infanticide risk is held constant at zero. Scenarios where the average female had less fewer than two surviving offspring are omitted from these plots (e.g. any time $p_{inf} > 0.10$).

benefits from the Bruce effect until monthly probability of infanticide is at or above 0.10. This discrepancy is most likely explained by differences in the absolute benefits calculated by the analytical model as compared to biologically relevant benefits generated in the individual-based model.

Two assumptions of the analytical and individual-based model are potentially unrealistic. First, the models assume that infanticide risk is constant each month from birth of the infant until its weaning or death if a mother experienced a male take-over during her pregnancy. This assumption may be unrealistic, both because older infants may become more resistant to infanticidal attack and because males have less to gain from infanticide as infants get older. To address this issue, I built an alternative model that treats infanticide risk as a linearly declining probability during each month after birth, such that infanticide risk declines over the 12-month period of dependence and reaches zero following weaning. The results of both the analytical and individual-based models under this assumption were qualitatively very similar to those presented in Figs 2 and 4, although the absolute benefits derived by females from avoiding infanticide are generally reduced (see Supplementary material 1, Figs S2 and S3).

Still, it is very likely that there exist many systems in which neither a constant risk of infanticide nor a linearly declining risk of infanticide following male take-over closely approximates the true risk to infants following male take-over. For example, some reports from studies of red howlers, *Alouatta seniculus*, and white-faced capuchins, *Cebus capucinus imitator*, indicate that infanticide risk is highest for the youngest infants in the group, although older infants still face substantial risk of infanticide (Agoramoorthy & Rudran, 1995; Brasington, Wikberg, Kawamura, Fedigan, & Jack, 2017). To maximize the predictive utility of the analytical model, I have included a tool in the supplement (see Supplementary material 2, Versatile Analytical Model.xlsx) that allows users to change the relationship between infant age and infanticide risk and then estimate the expected net temporal costs or benefits of the Bruce effect. This tool will allow researchers with data on relative infanticide risk at different ages to predict whether they expect the Bruce effect to have evolved in their system.

Another potentially unrealistic component of the individual-based model is the way in which it incorporates the risk of infanticide and feticide to mothers' survival. Although death occasionally appears to accompany feticidal and infanticidal attacks in baboons (Zipple et al., 2017), the risk of harm to mothers might better be modelled as a reduction in life span rather than an acute risk of death. I explored this possibility by replacing risk of death following feticidal or infanticidal loss with a definite loss of 3, 6 or 12 months of life. Again, the results from this alternative model were qualitatively consistent with the results in Figs 2 and 4, and are included in Supplementary material 1 (Fig. S4).

In addition to those factors explicitly considered in the model, additional ecological and life historical characteristics are likely to influence the net benefits that females derive from the Bruce effect. For example, the models presented consider investment in offspring to be exclusively temporal, but physical investment in offspring is a major component of female mammalian life history. As a result, females that invest more in offspring during pregnancy (e.g. species with a relatively high ratio of infant to mother body size) stand to lose more if their infants are killed, which might increase the benefits of the Bruce effect.

The modelling results described here are consistent with the limited data that exist from wild primate populations on the role of infanticide in the evolution of the Bruce effect. Yellow baboons, *Papio cynocephalus*, chacma baboons, *Papio ursinus*, and geladas *Theropithecus gelada*, all have gestation periods of approximately 6

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months and display about 12 months of postpartum amenorrhea (Busse & Hamilton, 1981; de Magalhaes & Costa, 2009; Gesquiere, Altmann, Archie, & Alberts, 2018; Gilbert & Gillman, 1952). The individual-based model, then, is well suited to explore the role of feticide and infanticide in the evolution of the Bruce effect in these species. How do the predictions of the model correspond with data from wild populations of these species?

First, in the yellow baboons of Amboseli, take-over of highly aggressive males results in infant death for about 1.9 infants out of 100 within 2 weeks of take-over, corresponding to a monthly probability of infanticide of 0.038 (Zipple et al., 2017). Similarly, in the chacma baboons of the Okavango Delta, I estimate the monthly risk of infanticide following male take-over using data from Palombit et al. (2000) and Robert Seyfarth, personal communication (see Supplementary material 1), to be between 0.03 and 0.05. Frequency of male take-over is quite high in Okavango, with p_{take} being about 0.10 (average tenure = 6 months; Palombit et al., 2000), and as a result infanticide by males is responsible for the majority of infant mortality in this population (Cheney et al., 2004). Still, except in those cases when maternal death following infanticide is high, the individual-based model predicts a net cost to females over their complete life span if they exhibit the Bruce effect under these conditions. Therefore, the model does not predict the evolution of the Bruce effect in yellow or chacma baboons, and the Bruce effect has not evolved in these species. Instead, demographic and behavioural evidence (Alberts et al., 1992; Pereira, 1983; Zipple et al., 2017) indicates that feticide occurs in yellow baboons and demographic evidence has shown an absence of the Bruce effect in chacmas (Beehner, Zipple, Roberts, & Alberts, 2019; J. C. Beehner, personal communication, 1 August 2019).

In contrast, gelada infants face a probability of death of approximately 0.50 in the 4 months following male take-over, corresponding to a monthly probability of death following take-over of approximately 0.16 (Beehner & Bergman, 2008). Both the analytical and the individual-based models predict a net positive effect of the Bruce effect in this range. Consistent with this expectation, the Bruce effect has been documented in geladas (Roberts et al., 2012), without any observed aggression from males to pregnant females following take-over (J. C. Beehner, personal communication, 1 August 2019). Injuries are known to occur following take-overs, but it is primarily directed towards lactating females and their offspring (Schneider-Crease et al., in press).

Outside of cercopithecines, lions, *Panthera leo*, provide the best test of the model presented here and the verbal models that preceded it. Male take-over leads to the death of nearly all cubs that are still nursing at the time of take-over (corresponding with a $p_{inf} > 0.20$), and take-overs are relatively uncommon (occurring ever 21–33 months, corresponding to a p_{take} of 0.02–0.03) (Pusey & Packer, 1984). Both the quantitative models here and the verbal models that preceded them would predict that the Bruce effect should occur in lions, and indeed demographic evidence indicates that the Bruce effect does occur in lions (Bertram, 1975).

A major result of the quantitative model that has not been previously considered by verbal models is that the risk of maternal death in association with an infanticidal or feticidal attack could result in fitness benefits to those females that avoid such attacks by exhibiting the Bruce effect. In nature, such an outcome could occur if a mother attempted to protect her infant from male aggression and as a result was herself the recipient of that aggression. Maternal death may be more likely in association with a feticidal attack, in which males are unable to attack a fetus without also attacking the pregnant female carrying the fetus.

While data on the risk of maternal death following feticidal or infanticidal attack is extremely limited, indirect evidence from yellow baboons suggests that several mothers in the Amboseli population may have died during or as a result of a feticidal or infanticidal attack by an immigrant male (Zipple et al., 2017), suggesting that maternal death associated with feticidal or infanticidal attacks is measurable and may represent a substantial cost of male take-over in this species. Injuries to mothers during infanticidal attacks have been documented in 15 species of primates (reviewed in Knott et al., 2019), again supporting the idea that feticidal and infanticidal attacks may have a nonzero physical cost to the mother's physical wellbeing and survival.

Causing the death of pregnant or lactating females may appear maladaptive for immigrant males. However, when tenure length is uncertain, a male cannot reliably expect to mate with a female that is pregnant or lactating at the time of his immigration in the absence of a feticidal or infanticidal attack. As a result, incidentally killing or injuring pregnant or lactating females during such an

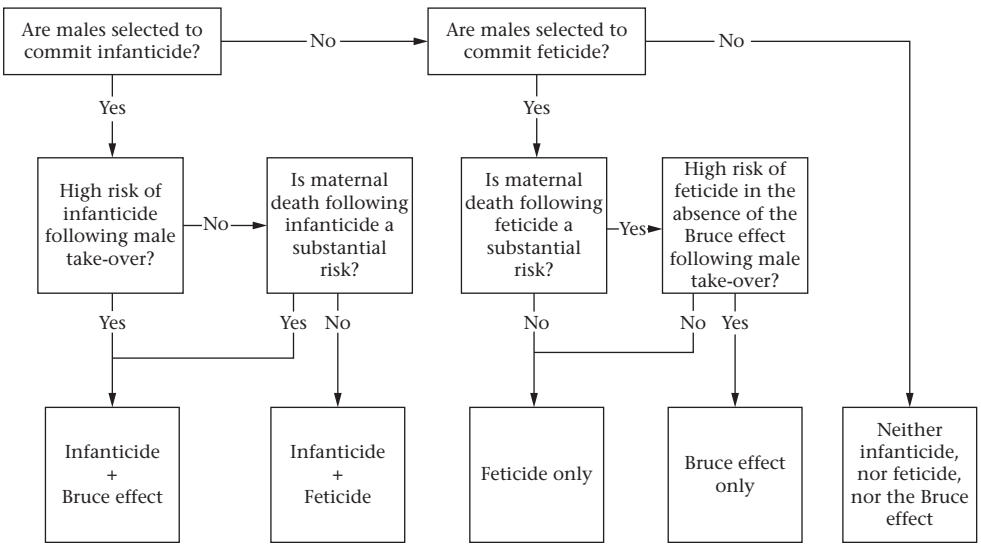

Figure 6. Predictions of whether infanticide, feticide and/or the Bruce effect will be present in study populations. Note that feticide and the Bruce effect are expected to be mutually exclusive phenomena and that feticide is expected to occur in all populations in which infanticide occurs, unless females evolve the Bruce effect.

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attack may represent only a minor cost to immigrant males relative to inaction.

The predictive power of the individual-based model is most strongly limited by the limited number of studies that have published evidence of fetal loss following male take-over or the likelihood of maternal death associated with feticidal or infanticidal loss. It would be of great utility to know how frequently rates of maternal death or disappearance increase following male take-over. Researchers may not currently be considering the possibility that disappearance of mothers is the result of male behaviour. The utility of this model can also be assessed by testing whether the Bruce effect occurs in species such as red howlers and hanuman langurs, both of which exhibit relatively high rates of infanticide following male take-over and low frequencies of male take-over (Agoramoorthy & Rudran, 1995; Hrdy, 1974, 1977; Sekulic, 1983). Such tests for the Bruce effect can be performed using demographic data (e.g. Bertram, 1975; Roberts et al., 2012), as the Bruce effect results in a pattern of a heavily depressed birth rate in the period following male take-over. Slight reductions in birth rate may instead indicate feticide in a population. A downside of a demography-only approach is that it assumes that feticide is unlikely to affect most or all females in a group because it involves targeted aggression, which may not be true under all circumstances. The best approach for distinguishing between the Bruce effect and feticide will involve the collection of both demographic data as well as dense behavioural data surrounding take-over events.

Zipple et al. (2019) previously hypothesized that feticide by males has been selected for across a broader range of the mammalian taxonomy than has infanticide by males. That hypothesis yielded the prediction that sexually selected feticide, but not infanticide, occurs in as-yet-unreported species and contexts. The present analysis leads to a new prediction: that the Bruce effect will evolve in the subset of these species in which feticide carries with it a substantial risk of maternal death. In species in which feticide does not carry a risk of maternal death, feticide will likely persist without the evolution of the Bruce effect. Overall, then, it is possible to make predictions as to whether feticide, infanticide and/or the Bruce effect is expected to be present in extant mammalian species depending on the parameters that I have discussed here (Fig. 6).

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2019.11.014.

References

Agoramoorthy, G., Mohnot, S. M., Sommer, V., & Srivastava, A. (1988). Abortions in free ranging hanuman langurs (*Presbytis entellus*): A male induced strategy? *Human Evolution, 3*(4), 297–308. https://doi.org/10.1007/BF02435859.

Agoramoorthy, G., & Rudran, R. (1995). Infanticide by adult and subadult males in free-ranging red howler monkeys, *Alouatta seniculus*, in Venezuela. *Ethology, 99*(1–2), 75–88. https://doi.org/10.1111/j.1439-0310.1995.tb01090.x.

Alberts, S. C., Sapolsky, R. M., & Altmann, J. (1992). Behavioral, endocrine, and immunological correlates of immigration by an aggressive male into a natural primate group. *Hormones and Behavior, 26*(2), 167–178. https://doi.org/10.1016/0018-506X(92)90040-3.

Bartoš, L., Bartošová, J., Chaloupková, H., Dušek, A., Hradecká, L., & Svobodová, I. (2016). A sociobiological origin of pregnancy failure in domestic dogs. *Scientific Reports, 6*, 22188. https://doi.org/10.1038/srep22188.

Bartoš, L., Bartošová, J., Pluháček, J., & Šindelářová, J. (2011). Promiscuous behaviour disrupts pregnancy block in domestic horse mares. *Behavioral Ecology and Sociobiology, 65*(8), 1567–1572. https://doi.org/10.1007/s00265-011-1166-6.

Beehner, J. C., & Bergman, T. J. (2008). Infant mortality following male takeovers in wild geladas. *American Journal of Primatology, 70*(12), 1152–1159. https://doi.org/10.1002/ajp.20614.

Beehner, J. C., Zipple, M. N., Roberts, E. K., & Alberts, S. C. (2019). A tale of three monkeys: Male-mediated prenatal loss explained. *American Journal of Physical Anthropology, 168*(Suppl. S68), 15.

Bertram, B. C. R. (1975). Social factors influencing reproduction in wild lions. *Journal of Zoology, 177*(4), 463–482. https://doi.org/10.1111/j.1469-7998.1975.tb02246.x.

Brasington, L. F., Wikberg, E. C., Kawamura, S., Fedigan, L. M., & Jack, K. M. (2017). Infant mortality in white-faced capuchins: The impact of alpha male replacements. *American Journal of Primatology, 79*(12). https://doi.org/10.1002/ajp.22725. e22725.

Bronson, F., & Eleftheriou, B. (1963). Influence of strange males on implantation in the deermouse. *General and Comparative Endocrinology, 3*, 515–518. https://doi.org/10.1016/0016-6480(63)90084-4.

Bruce, H. (1959). An exteroreceptive block to pregnancy in the mouse. *Nature, 184*(4680), 105.

Busse, C. D., & Hamilton, W. J. (1981). Infant carrying by male chacma baboons. *Science, 212*(4500), 1281–1283. https://doi.org/10.1126/science.212.4500.1281.

Cheney, D., Seyfarth, R., Fischer, J., Beehner, J., Bergman, T., Johnson, S., et al. (2004). Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. *International Journal of Primatology, 25*(2), 401–428. https://doi.org/10.1023/B:IJOP.0000019159.75573.13.

Crockett, C. M., & Janson, C. H. (2000). Infanticide in red howlers: Females group size, male membership, and a possible link to folivory. In C. P. van Schaik & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp. 75–98). Cambridge, U.K.: Cambridge University Press.

Eccard, J. A., Dammhahn, M., & Ylönen, H. (2017). The Bruce effect revisited: Is pregnancy termination in female rodents an adaptation to ensure breeding success after male turnover in low densities? *Oecologia, 185*(1), 81–94. https://doi.org/10.1007/s00442-017-3904-6.

Gesquiere, L. R., Altmann, J., Archie, E. A., & Alberts, S. C. (2018). Interbirth intervals in wild baboons: Environmental predictors and hormonal correlates. *American Journal of Physical Anthropology, 166*(1), 107–126. https://doi.org/10.1002/ajpa.23407.

Gilbert, C., & Gillman, J. (1952). Pregnancy in the baboon (*Papio ursinus*). *South African Journal of Medical Sciences, 16*(4), 115–124.

Hausfater, G. & Hrdy, S. (Eds.). (1984). *Infanticide: Comparative and evolutionary perspectives*. Hawthorne, NY: Aldine.

Hrdy, S. (1974). Male–male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatologica, 22*(1), 19–58. https://doi.org/10.1159/000155616.

Hrdy, S. (1977). Infanticide as a primate reproductive strategy. *American Scientist, 65*(1), 40–49.

Kenney, A. M., Evans, R. L., & Dewsbury, D. A. (1977). Postimplantation pregnancy disruption in *Microtus ochrogaster, M. pennsylvanicus* and *Peromyscus maniculatus*. *Reproduction, 49*(2), 365–367.

Knott, C. D., Scott, A. M., O'Connell, C. A., Scott, K. S., Laman, T. G., Riyandi, et al. (2019). Possible male infanticide in wild orangutans and a re-evaluation of infanticide risk. *Scientific Reports, 9*, 7806. https://doi.org/10.1038/s41598-019-42856-w.

Labov, J. B. (1981). Pregnancy blocking in rodents: Adaptive advantages for females. *American Naturalist, 118*(3), 361–371. https://doi.org/10.1086/283828.

de Magalhaes, J. P., & Costa, J. (2009). A database of vertebrate longevity records and their relation to other life-history traits. *Journal of Evolutionary Biology, 22*(8), 1770–1774. https://doi.org/10.1111/j.1420-9101.2009.01783.x.

Packer, C., & Pusey, A. E. (1984). Infanticide in carnivores. In G. Hausfater & S. B. Hrdy (Eds.), *Infanticide: Comparitive and evolutionary perspectives* (pp. 31–42). Hawthorne, NY: Aldine.

Palombit, R. A. (2015). Infanticide as sexual conflict: Coevolution of male strategies and female counterstrategies. *Cold Spring Harbor Perspectives in Biology, 7*(6), 1–31. https://doi.org/10.1101/cshperspect.a017640.

Palombit, R., Cheney, D. L., Fischer, J., Johnson, S., Rendall, D., Seyfarth, R. M., et al. (2000). Male infanticide and defense of infants in chacma baboons. In C. P. van Schaik & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp. 123–152). Cambridge, U.K.: Cambrige University Press.

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Pereira, M. E. (1983). Abortion following the immigration of an adult male baboon (*Papio cynocephalus*). *American Journal of Primatology, 4*(1), 93–98. https://doi.org/10.1002/ajp.1350040109.

Roberts, E. K., Lu, A., Bergman, T. J., & Beehner, J. C. (2012). A Bruce effect in wild geladas. *Science, 335*(6073), 1222–1225. https://doi.org/10.1126/science.1213600.

van Schaik, C. (2000). Social counterstrategies against male infanticide in primates and other mammals. In P. M. Kappeler (Ed.), *Primate males: Causes and consequences of variation in group composition* (pp. 34–52). Cambridge, U.K.: Cambridge University Press.

van Schaik, C. (Ed.). (2009). *Infanticide by males and its implications*. Cambridge, U.K.: Cambridge University Press.

Schneider-Crease, I., Chiou, K. L., Snyder-Mackler, N., Bergman, T. J., Beehner, J. C., & Lu, A. (2020). Beyond infant death: The hidden costs of male immigration in geladas. *Animal Behaviour, 159*, 89–95.

Schwagmeyer, P. L. (1979). The Bruce effect: An evaluation of male/female advantages. *American Naturalist, 114*(6), 932–938. https://doi.org/10.1086/283541.

Sekulic, R. (1983). Male relationships and infant deaths in red howler monkeys (*Alouatta seniculus*). *Zeitschrift für Tierpsychologie, 61*(3), 185–202. https://doi.org/10.1111/j.1439-0310.1983.tb01337.x.

Sommer, V. (1994). Infanticide among the langurs of Jodhpur: Testing the sexual selection hypothesis with a long-term record. In S. Parmigiani & F. S. vom Saal (Eds.), *Infanticide and parental care* (pp. 155–198). Chur, Switzerland: Harwood Academic.

Stehn, R. A., & Richmond, M. E. (1975). Male-induced pregnancy termination in the prairie vole, *Microtus ochrogaster*. *Science, 187*(4182), 1211–1213. https://doi.org/10.2307/1739501.

Storey, A., & Snow, D. (1990). Postimplantation pregnancy disruptions in meadow voles: Relationship to variation in male sexual and aggressive behavior. *Physiology & Behavior, 47*(1), 19–25. https://doi.org/10.1016/0031-9384(90)90037-5.

Zipple, M. N., Grady, J. H., Gordon, J. B., Chow, L. D., Archie, E. A., Altmann, J., et al. (2017). Conditional fetal and infant killing by male baboons. *Proceedings of the Royal Society B: Biological Sciences, 284*. https://doi.org/10.1098/rspb.2016.2561, 20162561.

Zipple, M. N., Roberts, E. K., Alberts, S. C., & Beehner, J. C. (2019). Male-mediated prenatal loss: Functions and mechanisms. *Evolutionary Anthropology, 28*(3), 114–125. https://doi.org/10.1002/evan.21776.

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