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Infanticide and infant defence by males—modelling the conditions in primate multi-male groups

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Abstract

Infanticide by primate males was considered rare if groups contain more than one adult male because, owing to lower paternity certainty, a male should be less likely to benefit from infanticide. Guided by recent evidence for strong variation of infanticide in primate multi-male groups, we modelled the conditions for when infanticide should occur for a group with a resident and an immigrant male. Setting the parameters (e.g. infant mortality, reduction of interbirth interval, life-time reproductive success, genetic representation) to fit the conditions most commonly found in nature, we develop a game-theoretic model to explore the influence of age and dominance on the occurrence of infanticide and infant defence. Male age strongly impacts the likelihood of an attack which is modified by the father's defence. If the new male is dominant he is likely to attack under most circumstances whereas a subordinate male will only attack if the father does not defend. These model scenarios fit the conditions under which infanticide is known to occur in primate multi-male groups and offer an explanation why infanticide is common in some multi-male groups and rare in others. Overall, the benefits for infanticidal males are strongly governed by a reduced interbirth interval while advantages via improved genetic representation in the gene pool contribute but a minor fraction.

Keyword: Primates; Infanticide; Direct benefits; Rank and age; Evolutionarily stable strategy

1. Introduction

The killing of infants by conspecific males has been reported for many animal species, mostly mammals, and seems to be particularly frequent in primates (e.g. Hausfater and Hrdy, 1984; Parmigiani and vom Saal, 1994; Ebensperger, 1998; Janson and van Schaik, 2000; van Schaik, 2000a). Of the five explanatory hypotheses put forward to explain infanticide (overview e.g. in Hrdy, 1979; Hausfater and Vogel, 1982), the most pertinent has proven to be the sexual selection hypothesis, which attributes infanticide to male–male competition for reproduction (Hrdy, 1974). According to this hypothesis, killing of an infant results in reproductive advantage for male mammals under the following conditions: (1) only unrelated infants are killed; (2) premature loss of an infant enables the mother to conceive the next infant sooner; (3) the males' chances of siring the next infant are high. In addition, it has been argued that by killing an unrelated infant, males increase their own relative, genetic representation in the population simply because they reduce the genetic representation of a competing male (Hrdy, 1974; Hausfater and Vogel, 1982). While this is certainly true, the magnitude of such an indirect benefit has not been explored and its importance especially in relation to a reduced interbirth interval is not clear.

Most data for primates (van Schaik, 2000b), carnivores (Pusey and Packer, 1994) and rodents (Blumstein, 2000) support the sexual selection hypothesis. They

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mainly refer to groups containing only one breeding male called one-male groups. From time to time, this male is replaced by a new male (e.g. Struhsaker, 1977; Sommer, 1988) who may attack and eventually kill infants. Mothers and other group members usually defend the infant and female–female coalitions are common in this context. However, male defence is considered more efficient and riskier to the attacker than female defence (Hrdy, 1974; van Schaik, 2000b) but in one-male groups the father will no longer be around to protect his progeny.

Previous models (Chapman and Hausfater, 1979; Hausfater et al., 1982; Breden and Hausfater, 1990) mainly referred to the best data available at that time, the records for Hanuman langurs (*Semnopithecus* (*Presbytis*) *entellus*) living at three different sites in India (Sugiyama, 1965; Mohnot, 1971; Hrdy, 1977). Perhaps because in these populations the one-male group type predominates, the models likewise assume one-male settings. Infanticide in multi-male groups was observed but considered to be less likely (e.g. Busse and Hamilton, 1981; Sekulic, 1983; Leland et al., 1984; Newton, 1988; van Schaik, 1996) because potential male defenders will increase the costs for and reduce the success rates of attackers. The chances seem smaller for an infanticidal male to sire the next infant and thus to benefit from infanticide. He risks killing his own offspring particularly if mating skew is low and male tenure is long.

It has recently been confirmed that infanticide may indeed occur in primate multi-male groups (e.g. de Ruiter et al., 1994; Borries, 1997; Palombit et al., 2000; Soltis et al., 2000) and that it may be in accordance with the sexual selection hypothesis (Borries et al., 1999a; Crockett and Janson, 2000). Males already residing in the group were observed to defend infants (Borries et al., 1999b; Palombit et al., 2000). The data now available reveal a large variation in the occurrence of infanticide within and between primate populations (cf. Janson and van Schaik, 2000). For instance, in some multi-male groups, no or less than about 10% of all live-born infants are killed and infanticide does not account for more than 20% of infant mortality (e.g. *Macaca* spp., *Papio anubis*, *Papio cynocephalus*). In other species (e.g. *Papio ursinus*, *Propithecus diadema*, *Semnopithecus entellus*) more than 10% of all infants born fall victim to infanticide, accounting for over 30% of the infant mortality. It is suggested that the number of adult males per group, male replacement rates and age at weaning are important factors contributing to this variation (e.g. Borries and Koenig, 2000; Janson and van Schaik, 2000). However, other factors may be equally or even more important. It is possible that low rates of infanticide are common in species where immigrant males enter at the bottom of the males' dominance hierarchy and it takes several years of residency to climb to the top, resulting in large age and rank differences between new immigrants and residents (e.g. Sprague et al., 1998; van Noordwijk and van Schaik, 2001). Accordingly, high rates could prevail when new males attain top rank right after immigration (e.g. Borries, 2000; Palombit et al., 2000). These newcomers tend to be young adult males so that depending on immigration rates, rank and age differences may be comparatively small. Thus the mode of male immigration may act on the relative age and rank of competing males in multi-male groups. Paternity certainty, actual paternity (reproductive skew), residual reproductive value, risk of being injured in a conflict and with these the costs and benefits of infanticide and infant defence should depend upon age and rank in a predictable way. Hence, the effects of age and rank can be explored theoretically.

The present paper addresses these questions via mathematical modelling. Specifically: What are the conditions for the occurrence of infanticide and infant defence by males living in multi-male groups? We look at the simplest multi-male situation, that of a group containing two males. We will particularly consider the impact and relative importance of male age and dominance rank, a reduced interbirth interval, and alterations in the relative gene frequencies in the gene pool. Although we refer to non-human primates, the model can be adapted to the parameter settings of other mammalian species.

2. The model

2.1. General assumptions

We consider the smallest multi-male group possible. It is composed of two adult males, a variable number of adult females and one infant, the potential target of infanticide. There may be additional infants but we concentrate on this particular one. One of the males has been resident for some time and is or assumes that he is the father of the infant. He will be called the father (f). The other male has recently migrated into the group. He is not the father of the infant and may attempt to attack and kill it. He is called the new male (n). We do not assume conscious processes here, but generalize from field observations (Borries et al., 1999b). On the one hand, males who mate with a female during her conceptional period sometimes subsequently defend her infant. On the other hand, males who did not mate then are never observed to defend the infant, and sometimes attack it. In particular, each male has two strategies available to him. The new male can either attempt infanticide or not, and if an attempt is made, the father can defend the infant or not. The game can thus be expressed as an extensive form game with sequential decision-making (Selten, 1983). The new male makes his decision first, the father second; thus using the standard dynamic programming technique, we find the optimal strategy of the father conditional upon an attack being made, the new male then being able to choose whether to attack or not, depending upon what strategy the father will play. It should be noted that real behaviour may be more complex with several stages of escalation possible and that we have reduced the process to the simplest case, which retains the key features of whether to attack and whether to defend in the face of an attack. This yields a composite evolutionarily stable strategy, which tells us how a male in either position should behave, under any circumstances.

Infanticide may involve several unsuccessful attacks by the male (e.g. Borries, 1997; Palombit et al., 2000; Soltis et al., 2000). In our model an attack is thus defined as the whole period from the moment when the new male begins to attack the infant until he either gives up permanently or kills it. It is further assumed that the mother and possibly some of the other females try to defend the infant so that there is always some risk involved in attacking an infant.

2.2. *Defining male benefits*

We consider the expected reward E to either male as a function of the expected number of his infants, i, which reach maturity and the total (effective) population size, y, composed of all individuals in direct competition with each other as part of the same gene pool.

$$E(i, y) = iR(y)$$

where R is a competition function which decreases as y increases. As the population gets larger, there is more competition and thus reduced representation.

All benefits are given relative to those at the current population size x. An infant which reaches maturity when the population size is x is worth payoff 1 to its father. Thus we set $R(x) = 1$. This standardization is possible since $R(x)$ only influences our analysis through the factor I which depends upon the relative size of $R(x)$ and $R(x-1)$ only (see Table 1).

If there is sufficient food, so that competition over food is irrelevant and the population has room to increase in numbers, then strict numbers are more important than the proportion of the gene pool and so $R(y) = 1$, independent of y.

However, if the population cannot expand as is the case for most natural populations that live close to the carrying capacity, the proportion of the gene pool becomes more important and $R(y)$ is proportional to

$\frac{1}{y}$ i.e. $R(y) = \frac{x}{y}$.

Reality may lie somewhere between these two extremes, i.e.

$$R(y) = \varphi \frac{x}{y} + (1 - \varphi)$$

with $0 < \varphi < 1$, a constant factor; the larger the value of φ, the more intense the competition.

2.3. *Parameters*

The general characteristics of the model population are given in Table 1. These parameters will obviously vary according to species, dominance effects, number of females, etc. It is likely that:

$g(t)$ is a decreasing function of t, tending to 0 for large t. The younger a dependent infant dies, the shorter the inter-birth interval of its mother (Altmann et al., 1977; Sommer, 1994; Borries, 1997);

the injury probabilities q_1, q_3 are relatively small. In fact, very few cases are reported for primates (van Schaik, 2000b);

$v > q_1 + q_2$ so that the probability of the infant being killed is reduced (markedly) if the father defends. Here, we follow the assumption of several researchers (Altmann, 1990; Newton and Dunbar, 1994; van Schaik, 1996);

$A_f + E_f + \alpha + \beta(t)$ is the father's total expected number of infants surviving to maturity (for the new male it is $A_n + E_n$). This formula gives his lifetime reproductive success, if no infanticide or injury results from the present encounter (if infanticide or injury does occur, then these formulas vary according to Table 2);

the ratio of expected to existing offspring varies with the age of the males and $A > E$ for an old male while $A < E$ for a young male;

a male's rank will act on the paternity probability and on the risk of injury with p being small, $q_1 > q_3$ if the father is subordinate and p being large, $q_1 < q_3$ if the father is dominant while p will be intermediate, $q_1 = q_3$ if there is no rank effect.

2.4. *Benefits under different circumstances*

In case an attack occurs and the father defends, both males are faced with a particular risk of being injured. For reasons of simplicity, we assume that injury is equivalent to disappearance or death of the adult male and a residual reproductive value E of zero, an extreme though likely consequence in primates (e.g. Sommer, 1988). If the father is injured during defence, the infant is killed, while if the new male is injured the infant survives. The lifetime reproductive success of each of the two males under the different circumstances is summarized in Table 2. It is composed of the number of already

Table 1
Parameters of the model population

Parameter	Description
1. *General parameters*	
x	Effective population size before any attack (see also text)
$R(y)$	Interference function assuming effective population size y (by a simple scaling we can assume $R(x) = 1$ for our given x)
A_f	Expected number of offspring of the father to survive to maturity out of those which have already been born, not including the target infant
E_f	Expected number of future offspring of the father to survive to maturity, assuming that no infanticide occurs (equals his residual reproductive value, Fisher, 1930)
A_n	Expected number of offspring of the new male to survive to maturity out of those which have already been born.
E_n	Expected number of future offspring of the new male to survive to maturity, assuming that no infanticide occurs, his residual reproductive value.
p	Probability that the mother's next infant is sired by the original father if the target infant is killed and neither male is injured
α	Probability that a newborn infant survives to maturity which is assumed to be similar for the next infant or any extra infant born after infanticide and identical for both males and thus independent of fatherhood
$\alpha+\beta(t)$	Probability that the target infant aged t survives to maturity if it is not killed in an attack, where $\beta(t)$ is an increasing function of t.
v	Probability that the infant is killed if only females defend
2. *Parameters when the father defends*	
q_1	Probability that the father is injured and the infant is killed
q_2	Probability that neither male is injured, but the infant is killed
q_3	Probability that the new male is injured and the infant survives
$1-q_1-q_2-q_3$	Probability that the infant survives and neither male is injured
3. *Reproductive and competitive effects*	
$g(t)$	Average number of extra births due to the death of an infant aged t years; for instance, if the mean interbirth interval is 2.4 years and this is reduced by 1.2–0.6t years on average for an infant aged $t<2$ years as occurs in Hanuman langurs (Borries, 1997), then $g(t) = \frac{1}{2.4}(1.2 - 0.6t) = (0.5 - 0.25t) \quad t \leqslant 2$
$I = \frac{R(x-1)-R(x)}{R(x-1)}$	Decrease in competition in the population after a death; it is the ratio of the increase in value of an individual as the population decreases from size x to size $x-1$, and the absolute value of the individual for the new population size. As shown in the text, the function $R(y)$ only affects the optimal behavior through the value of I.

Note. Parameters when the father defends exclude two possibilities (father injured and infant survives, and new male injured and the infant is killed) which involve a decisive victory by one male in their individual contest but the winner does not get his way in the fate of the infant which we consider unlikely and so have ignored for simplicity.

Table 2
Rewards for the father and the new male under different circumstances

Circumstances				Rewards for		Probability
New male attacks	Father defends	Male injured	Infant killed	Father	New male	given the attack/defence situation
No	No	No	No	$(A_f + E_f + \alpha + \beta(t))R(x)$	$(A_n + E_n)R(x)$	1
Yes	No	No	Yes	$[A_f + E_f + g(t)p\alpha]R(x-1)$	$[A_n + E_n + g(t)(1-p)\alpha]R(x-1)$	v
Yes	No	No	No	$(A_f + E_f + \alpha + \beta(t))R(x)$	$(A_n + E_n)R(x)$	$1-v$
Yes	Yes	Father	Yes	$A_f R(x-1)$	$[A_n + E_n + g(t)\alpha]R(x-1)$	q_1
Yes	Yes	No	Yes	$[A_f + E_f + g(t)p\alpha]R(x-1)$	$[A_n + E_n + g(t)(1-p)\alpha]R(x-1)$	q_2
Yes	Yes	New male	No	$(A_f + E_f + \alpha + \beta(t))R(x)$	$A_n R(x)$	q_3
Yes	Yes	No	No	$(A_f + E_f + \alpha + \beta(t))R(x)$	$(A_n + E_n)R(x)$	$1-q_1-q_2-q_3$

existing offspring A plus the future offspring E, modified by the competition function R. Furthermore, if the target infant survives (no or unsuccessful attack) it is added to the father's reproductive success modified by its chances to survive $\alpha+\beta(t)$. If the target infant is killed an extra infant is added to either male with probability equal to $g(t)$, modified by the newborn infant's probability of survival α and by the probability of paternity p. Competition in the population is reduced to $R(x-1)$.

We now find the conditions for infanticide and infant defence, i.e. two conditions are distinguished in the model population:

A. Condition A indicates under which circumstances it is best for the father to defend if there is an attack. If A holds, this implies that the father should defend the infant whereas, if $\bar{A}$ holds (A does not hold), he should not.
B. Condition B indicates when it is best for the new male to attack, assuming there will be defence by the father. If there will be no defence then there remains only the risk of injury via female defence, which for reasons of simplicity is assumed to be zero, so an attack would always be best (but see below). If B holds, this implies that the new male should attack the infant, whereas if $\bar{B}$ holds, he should not.

This argument generates three possible situations:

(1) $\bar{A} \Rightarrow$ new male attacks, father does not defend;
(2) $A \cup B \Rightarrow$ new male attacks, father defends;
(3) $A \cup \bar{B} \Rightarrow$ new male does not attack.

Weighting the various possible rewards from Table 2 by the probability of their occurrence, the reward to the father is,

$$\begin{aligned}&q_1 A_f R(x-1) + q_2[E_f + A_f + g(t)p\alpha]R(x-1)\\&\quad + q_3(E_f + A_f + \alpha + \beta(t))R(x)\\&\quad + (1 - q_1 - q_2 - q_3)(E_f + A_f + \alpha + \beta(t))R(x)\end{aligned}$$

if he defends, and $v[E_f + A_f + g(t)p\alpha]R(x-1) + (1 - v)(E_f + A_f + \alpha + \beta(t))R(x)$ if he does not. A occurs if the benefit to the father is greater if he defends than if he does not, i.e.

$$\begin{aligned}&q_1 A_f R(x-1) + q_2[E_f + A_f + g(t)p\alpha]R(x-1)\\&\quad + q_3(E_f + A_f + \alpha + \beta(t))R(x)\\&\quad + (1 - q_1 - q_2 - q_3)(E_f + A_f + \alpha + \beta(t))R(x)\\&\quad > v[E_f + A_f + g(t)p\alpha]\\&R(x-1) + (1 - v)(E_f + A_f + \alpha + \beta(t))R(x)\\&\quad \Rightarrow (E_f + A_f + \alpha + \beta(t))[R(x) - R(x-1)](v - q_1 - q_2)\\&\quad - (\alpha + \beta(t))R(x-1)(q_1 + q_2 - v) - q_1 E_f R(x-1)\\&\quad + g(t)p\alpha R(x-1)(q_2 - v) > 0.\end{aligned}$$

Setting $I = [R(x-1) - R(x)]/R(x-1)$ implies that A occurs if

$$\begin{aligned}&(E_f + A_f + \alpha + \beta(t))(v - q_1 - q_2)I + g(t)p\alpha(v - q_2)\\&\quad - [(\alpha + \beta(t))(v - q_1 - q_2) - q_1 E_f] < 0.\end{aligned}$$

B occurs if the benefit to the new male is greater if he attacks, assuming that the father defends, than if he does not attack. Similarly weighting the rewards from Table 2 for the new male, we obtain B if

$$\begin{aligned}&q_1(E_n + A_n + g(t)\alpha)R(x-1)\\&\quad + q_2(E_n + A_n + g(t)(1-p)\alpha)R(x-1) + q_3 A_n R(x)\\&\quad + (1 - q_1 - q_2 - q_3)(E_n + A_n)R(x) > (E_n + A_n)R(x)\end{aligned}$$

$$\begin{aligned}&\Rightarrow (E_n + A_n)(q_1 + q_2)[R(x-1) - R(x)] - q_3 E_n R(x)\\&\quad + g(t)\alpha R(x-1)[q_1 + q_2(1-p)] > 0\end{aligned}$$

dividing by $R(x-1) \Rightarrow [(E_n + A_n)(q_1 + q_2) + q_3 E_n]I + g(t)\alpha[q_1 + q_2(1-p)] - q_3 E_n > 0.$

These inequalities indicate how the values of the different parameters influence the likelihood of the new male to attack and the father to defend (Table 3). Of course, some of these parameters are not independent and are heavily influenced by the dominance ranks of the males. This is apparent in the following examples which illustrate some of the key predictions of the model.

The above inequalities A and B are linear in the terms $g(t)$ and I and so these terms affect the propensity for attack and defence in a straightforward way. Fixing all the above parameters in the two equations (i.e. leaving them at a constant value while varying the chosen ones) reveals that both attack and no defence are favoured by larger I and larger $g(t)$, so that infanticide is more likely the larger these are. Since the new male's gain (through $g(t)$) is largest for small values of t, males should preferentially attack young infants. Note that for the father, the loss is larger for older infants (their survival rate is better) so that defence is more important then. The difference in competition due to the death of a single individual (I) is largest for a population low in number, with a small gene pool.

Table 3
The influence of parameters on attack and defense conditions

Parameter	A holds: father defends if	B holds: new male attacks if
$\alpha+\beta(t)$	Large	
v	Large	
q_1	Small	Large
q_2		Large
q_3		Small
$v-q_1-q_2$	Large	
p	Small	Small ($1-p$ = large)
α	Small	Large
E	Small	Small
$g(t)$	Small	Large
I	Small	Large

Note. In each case "small" and "large" mean that the smaller (larger) the respective parameter the more likely will be attack by the new male or defence by the father. $v - q_1 - q_2$ the value of the increase in the probability that the target infant survives when the father defends.

3. Examples

To explore the effect of male age and dominance on the occurrence of attack and defence and to simulate natural scenarios for different primate species we calculate several examples. In these examples the following factors are considered constant. φ is set to equal 1. The population size is moderate ($x = 1000$) resulting in a value of the competition function

$$R(y) = \frac{1000}{y}, \quad \text{i.e. } I = \frac{R(999) - R(1000)}{R(999)} = 0.001.$$

The probability of survival to maturity for newborn infants is set to $\alpha = 0.5$, a value most commonly found in undisturbed primate populations (e.g. Altmann et al., 1978; Borries and Koenig, 2000; Palombit et al., 2000). The probability of survival to maturity for the target infant provided there is no infanticide varies with age of the infant with $\beta(t) = 0.2t$ and $t<2$. Note that the oldest monkey killed by a male was 18 months old and the oldest ape 21 months (van Schaik, 2000b) and most monkeys terminate infancy before turning 2 years of age. The expected number of extra births if infanticide occurs is $g(t) = 0.5 - 0.25t$ $t<2$ (cf. above).

It is reported in Sommer (1994) that out of 110 infants exposed to a new male in single male groups (so that only female defence was available), 53 were observed to be attacked of which 39 were killed (35% of the total, 74% of those seen to be attacked). Given that many attacks go unobserved, but all fatalities are observed, 74% is likely to be a significant overestimate of the success percentage. In our examples we set the probability that the target infant is killed if only females defend as $v = 0.5$. Both males are assumed to have a similar life-time reproductive success of $E_f + A_f = E_n + A_n = 5$, a likely mean value for stable primate populations which usually contain more adult females than adult males. In fact the father's life-time reproductive success is $A_f + E_f + \alpha + \beta(t)$ and so is a little higher than the new male's.

All other factors vary depending on the age and rank of the males. Age affects the residual reproductive value (E), while rank is assumed to affect the relative probability of being injured (q_1 and q_3), the probability that the infant is killed $q_1 + q_2$ if the father defends, and the reproductive skew expressed via p.

3.1. *Examples 1—males evenly matched (same rank)*

Under some conditions male reproductive success does not depend on dominance (e.g. Shively and Smith, 1985; Berard et al., 1993; Paul and Kuester, 1996). Even though most of these paternity data stem from captive or semi-free ranging primates, in some societies male dominance rank seems of little importance (Strier, 1994). Similar rank implies identical risk of injury and identical paternity probability. Hence, $q_1 = q_3 = 0.02$, $q_2 = 0.38$ (so $q_1 + q_2 = 0.4$), $p = 0.5$. For these examples, the two conditions thus reduce to A occurs if $0.1(5.5 + 0.2t) \times 0.001 + 0.03(0.5 - 0.25t) - [0.1(0.5 + 0.2t) - 0.02\,E_f] = -0.03445 + 0.02\,E_f - 0.02748t < 0$ and B occurs if $[2 + 0.02\,E_n] \times 0.001 + 0.105(0.5 - 0.25t) - 0.02\,E_n = 0.0545 - 0.01998\,E_n - 0.02625t > 0$.

Because there is no a priori justification for male age we explore the effect of age of the two males on defence and attack patterns for all four extreme combinations:

(i) Both males are young, $E_f = En = 4$; then A: $-0.03445 + 0.02 \times 4 - 0.02748t < 0 \Rightarrow t > 1.66$

B: $0.0545 - 0.01998 \times 4 - 0.02625t > 0 \Rightarrow B$ does not hold i.e. $t < 1.66$ new male attacks, father does not defend; $t > 1.66$ no attack.

(ii) Both males are old, $E_f = E_n = 1$; then A always holds, B holds if $t < 1.32$ i.e. $t < 1.32$ new male attacks, father defends; $t > 1.32$ no attack.

(iii) The father is old, the new male young, $E_f = 1$, $E_n = 4$; then A always holds, B does not hold, i.e. there is no attack.

(iv) The father is young, the new male old, $E_f = 4$, $E_n = 1$; then A holds if $t > 1.66$, B holds if $t < 1.32$ i.e. $t < 1.66$ new male attacks, father does not defend; $t > 1.66$ no attack.

These examples show that the defence of fathers depends on their residual reproductive value. If it is low, the value of the target infant might become decisive. In other words older fathers are more likely to defend young infants than younger fathers. The latter may only defend old infants. Male attack similarly depends on the residual reproductive value, i.e. B does not hold for young males and they would only attack, if fathers do not defend. In contrast, old males may attack despite defence of (old) fathers.

3.2. *Examples 2—males not evenly matched (difference in rank)*

Most studies of wild primates have shown that male reproductive success depends on dominance rank with the highest ranking male, the alpha male being most successful (e.g. de Ruiter et al., 1994; Bercovitch and Nürnberg, 1997; Gust et al., 1998; Launhardt et al., 2001). These societies may differ, however, in male migration pattern. In some populations males in their prime age immigrate and take over the alpha position from older males (Borries, 2000; Palombit et al., 2000). Depending on the turn-over rate for the alpha position, the difference in age might only be small. In other cases young males enter the hierarchy at the bottom (Sprague et al., 1998; van Noordwijk and van Schaik, 2001) or older males frequently change groups (Alberts and Altmann, 1995; Borries, 2000). Unequal dominance rank is likely to translate into different risks of injury with the dominant male facing a smaller risk. The reproductive skew (p) will also be altered. In addition, the probability that the infant is killed with no male injured (q_2) may change, and with it the overall probability that the infant is killed in an attack (q_1+q_2). However, since this sum mainly affects the results through ($v-q_1-q_2$), we shall not alter it for simplicity. Even though other scenarios may be possible, the examples below are the most likely scenarios among nonhuman primates. In each case we return to the original conditions A and B to find the optimal behaviour.

Examples 2a—father subordinate: (i) The father is subordinate and old, the new male is dominant and young, with $q_1=0.03$, $q_3=0.01$, $q_2=0.37$ (so $q_1+q_2=0.4$), $p=0.2$, $E_f=1$, $E_n=4$; then A always holds, B holds if $t<1.07$ i.e. $t<1.07$ new male attacks, father defends; $t>1.07$ no attack.

(ii) The father is subordinate but only slightly older than the new male who is dominant and young, with $q_1=0.03$, $q_3=0.01$, $q_2=0.37$ (so $q_1+q_2=0.4$), $p=0.2$, $E_f=2$, $E_n=4$; then A holds if $t>0.73$, B holds if $t<1.07$, i.e. $t<0.73$ new male attacks, father does not defend; $0.73<t<1.07$ new male attacks, father defends; $t>1.07$ no attack.

If young males immigrate and attain the alpha position, they attack only young infants and they do so even if the father defends. A subordinate father defends infants of high residual reproductive value. Infants of low residual reproductive value are only defended if the father is at the end of his reproductive career. Thus under the condition of high male immigration rates of relatively young males especially young infants seem to be at risk of being killed and more so if their father is only slightly older than the new male.

Examples 2b—father dominant: (i) The father is dominant and old, the new male is subordinate and young, with $q_1=0.01$, $q_3=0.03$, $q_2=0.39$ (so $q_1+q_2=0.4$), $p=0.8$, $E_f=1$, $E_n=4$; then A always holds, B does not hold, i.e. there is no attack.

(ii) The father is dominant and young, the new male is subordinate and old, with $q_1=0.01$, $q_3=0.03$, $q_2=0.39$ (so $q_1+q_2=0.4$), $p=0.8$, $E_f=4$, $E_n=1$; then A holds if $t>0.41$, B does not hold, i.e. $t<0.41$ new male attacks, father does not defend; $t>0.41$ no attack.

Under the condition that subordinate males immigrate there is little prospect of attacks, particularly if the new males are young. Fathers are ready to defend and it especially does not pay a new young subordinate male to attack infants. Only if the father is young and the new subordinate male old may the latter attack the infant. Under such a condition a father might not defend young infants and an old male might take advantage of this condition, even if his chances of siring the next infant are low.

4. Benefits for new males

Infanticidal males will gain advantages via a reduced interbirth interval ($g(t)$) and the reduction in competition (I). Their relative contribution will be explored in the following. As indicated above, the benefit is given as

$$R(y)=\varphi\frac{x}{y}+(1-\varphi),\quad 0<\varphi<1 \text{ then}$$

$$I=\frac{R(x-1)-R(x)}{R(x-1)}\Rightarrow$$

$$I=\frac{\varphi\frac{x}{x-1}+(1-\varphi)-1}{\varphi\frac{x}{x-1}+(1-\varphi)}=\frac{\varphi[x-(x-1)]}{(x-1)(1-\varphi)+x\varphi}=\frac{\varphi}{x-(1-\varphi)}.$$

The largest plausible value of I is $1/x$, and it may well be a lot smaller. Thus, for a population of 1000 individuals, $I<0.001$. The reduced interbirth interval $g(t)$ typically may range from 0 to 0.5 (cf. Struhsaker and Leland, 1987; van Schaik, 2000b). When the reduced interbirth interval is an important factor, the interference term is dwarfed by it, and so at most adds a small secondary benefit. For example in Example 1(i), in the case of a newborn infant, the numerical value in the equation for conditions A of the term including I is 0.00085 and the corresponding value for the term including $g(t)$ is 0.015. Similarly, the contributions of the terms including I and $g(t)$ in the equation for condition B are 0.00328 and 0.0525, respectively. In each case the contribution of reduced interbirth interval is 16 times higher than the competition term. In the other examples the difference is even more extreme. This tendency is even stronger for larger and probably more natural population sizes. As long as there is a noticeable advantage gained via a reduction in the subsequent interbirth interval indirect benefits seem to be of minor importance.

To explore the effect of mere indirect benefits we consider $g(t)\equiv 0$, i.e. the interbirth interval is not reduced by infanticide.

Then A becomes $(E_f+A_f+\alpha+\beta(t))(v-q_1-q_2)I-[(\alpha+\beta(t))(v-q_1-q_2)-q_1E_f]<0$

B becomes $[(E_n+A_n)(q_1+q_2)+q_3E_n]I-q_3E_n>0$

The father will only not defend (A not satisfied) if the second term is negative, which occurs only if the father runs a large risk of injury in defence without giving much extra protection to what the female coalition would. So it is very likely that the father defends the infant. B will only occur if the new male's risk of injury is extremely (unfeasibly) small. As soon as an even small risk of an injury being received when female defence occurs, the new male should not attack. Since the father will defend in most scenarios, an attack seems very unlikely when the interbirth interval is not reduced.

5. Conclusions

5.1. Age effects

Age, primarily via its effect on a male's residual reproductive value, has a major influence on the occurrence of attacks and defence (Examples 1). In multi-male groups primarily old males should attack infants, although this trend is modified by the father's defence. A young father will only protect older infants, thus facilitating attacks on young infants. The situation culminates when two old males are in confrontation. They will both be prepared to take high risks so that infants will always be defended, young infants will be attacked despite defence and only older infants will not be attacked. Intuitively, these results seem to make sense. Among primates, however, old males have not been reported to attack infants disproportionately. Migrating older males are often subordinate and so less likely to attack; if males beyond prime age kill infants it is usually because they have recently risen in rank (Soltis et al., 2000). The lack of support of the model is most likely due to a lack of pure age effects among primate males, since contests between evenly matched males are quite rare. Pure age effects therefore clearly deserve further attention to test this aspect of the model appropriately.

5.2. Dominance effects

Introducing dominance effects and with it a reproductive skew lets new males (young and dominant) attack despite defence by the father (cf. example 2a(i)). That is, it pays incoming males to attack and kill infants, especially young infants. If the age difference between father and new male is only modest (example 2a(ii)), the new male's risk is reduced when attacking young infants because they will not be defended by the father. For subordinate fathers defence depends on their residual reproductive value. A low value renders defence more likely.

In general any factor which has an effect on the values of our parameters will influence the optimal behaviour. A new male attaining top dominance right after immigration is typical for chacma baboons (*P. ursinus*) at the Moremi Game Reserve, Botswana or Hanuman langurs (*S. entellus*) of Ramnagar, Nepal (Borries, 2000; Palombit et al., 2000). Consequently infanticide is common and its impact on infant mortality is high.

The situation should be markedly different for new males immigrating as subordinates. Their decision to attack should entirely depend on the father's behaviour and they will only attack if he does not defend which holds true for young fathers with young infants whereas old fathers will always defend. In several primate multi-male groups it is common for immigrant males to attain subordinate ranks (e.g. *Macaca fuscata*, Sprague et al., 1998; *Macaca fascicularis*, van Noordwijk and van Schaik, 2001). They are confronted with dominant and usually older resident males, circumstances for which no infanticide is predicted. And indeed, infanticide seems to be rare in these species. The reported cases of males attacking infants all happened under exceptional circumstances that seem to fit the predictions, after the four highest-ranking males (the most likely fathers) had left the group (Soltis et al., 2000) and after the attackers had rapidly risen in rank (de Ruiter et al., 1994). However, it is currently not known whether young fathers will indeed not defend very young infants.

These examples suggest that the observed variation of infanticide in primate multi-male groups may be explained by differences in male migration pattern and the resulting differences in age and dominance rank of competing males.

5.3. Balancing benefits

Male benefits derived from infanticide are mainly influenced by a direct reproductive advantage attained via the prospect of siring an extra infant. The conditions under which the evolutionarily stable strategy would indicate that infanticide would occur even if it renders only an indirect advantage are rather narrowly defined: the attacker's risk has to be very small. Perhaps the few observed cases when males attacked infants residing in neighbouring groups fit this scenario (e.g. Borries, 1997). The recently described case of infanticide in patas monkey (*Erythrocebus patas*, Enstam et al., 2002) might be another example for exceptional circumstances. A single male in a group of females killed an infant although the subsequent interbirth interval was not shortened in this seasonally and annually breeding species. It is likely that patas males, when alone in a group of females, face a very low risk of being injured indicated by a rather high general canine dimorphism index (GCDI) and one of the highest body weight dimorphisms amongst anthropoid primates (Plavcan and van Schaik, 1992, 1997). Mere indirect advantages might, furthermore, be sufficient if the population size is very small (e.g. in populations close to extinction). It is, however, not clear whether this situation occurs in nature.

More generally, in multi-male groups with little prospect of direct benefits, a male is expected to refrain from attack if he would risk being injured. Since females almost always defend and defence by fathers is very likely (if their costs are small or moderate), new immigrant males will not attack. Mere indirect benefits are most probably not sufficient to explain the evolution of infanticide by males.

5.4. Perspectives

So far we have restricted our exploration to the smallest multi-male group possible, a single father and a second male as a new immigrant. The situation will be much more complex when considering additional male residents and is strongly influenced by mating skew and paternity probability. Furthermore, the duration of male tenure (in relation to paternity probability) will act on the number of infants exposed to immigrant males and on the number of male defenders available (e.g. Borries and Koenig, 2000). Finally, immigration by male coalitions (e.g. *Alouatta seniculus*, Pope, 2000) and cooperative female defence in relation to female group size will affect the probability of attacks. Thus, even though the model provides a first step towards explaining variable rates and frequencies of infanticide among multi-male groups, inclusion of further variables is clearly desirable. We furthermore hope that more and detailed data will soon become available to allow the model to be tested.

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