Broom, M., Borries, C. & Koenig, A. (2004). Infanticide and infant defence by males--modelling the conditions in primate multi-male groups. Journal of Theoretical Biology, 231(2), 261 - 270. doi: 10.1016/j.jtbi.2004.07.001 <http://dx.doi.org/10.1016/j.jtbi.2004.07.001>

CITY UNIVERSITY LONDON

City Research Online

Original citation: Broom, M., Borries, C. & Koenig, A. (2004). Infanticide and infant defence by males--modelling the conditions in primate multi-male groups. Journal of Theoretical Biology, 231(2), 261 - 270. doi: 10.1016/j.jtbi.2004.07.001 <http://dx.doi.org/10.1016/j.jtbi.2004.07.001>

Permanent City Research Online URL: http://openaccess.city.ac.uk/986/

1   **Infanticide and infant defence by males -**

2   **modelling the conditions in primate multi-male groups**

3

4   **MARK BROOM***, **CAROLA BORRIES**† & **ANDREAS KOENIG**†

5

6   * Centre for Statistics and Stochastic Modelling, School of Mathematical Sciences,

7   University of Sussex, Falmer, Brighton BN1 9QH

8   † Department of Anthropology, Stony Brook University, Stony Brook NY 11794-4364, USA

9

10   Running headline: Infanticide in multi-male groups

11

12   *Correspondence: M. Broom, Centre for Statistics and Stochastic Modelling, School of*

13   *Mathematical Sciences, University of Sussex, Brighton BN1 9QH, UK, phone: +44-1273-*

14   *877243; fax: +44-1273-678097, e-mail: M.Broom@sussex.ac.uk*

15

17

18

19   **Abstract**

20   Infanticide by primate males was considered rare if groups contain more than one adult male

21   because, owing to lower paternity certainty, a male should be less likely to benefit from

22   infanticide. Guided by recent evidence for strong variation of infanticide in primate multi-

23   male groups, we modelled the conditions for when infanticide should occur for a group with a

24   resident and an immigrant male. Setting the parameters (e.g. infant mortality, reduction of

25   interbirth interval, life-time reproductive success, genetic representation) to fit the conditions

1 most commonly found in nature, we develop a game-theoretic model to explore the influence

2 of age and dominance on the occurrence of infanticide and infant defence. Male age strongly

3 impacts the likelihood of an attack which is modified by the father's defence. If the new male

4 is dominant he is likely to attack under most circumstances whereas a subordinate male will

5 only attack if the father does not defend. These model scenarios fit the conditions under

6 which infanticide is known to occur in primate multi-male groups and offer an explanation

7 why infanticide is common in some multi-male groups and rare in others. Overall, the

8 benefits for infanticidal males are strongly governed by a reduced interbirth interval while

9 advantages via improved genetic representation in the gene pool contribute but a minor

10 fraction.

11

12 **Introduction**

13 The killing of infants by conspecific males has been reported for many animal species,

14 mostly mammals, and seems to be particularly frequent in primates (e.g. Hausfater & Hrdy,

15 1984; Parmigiani & vom Saal, 1994; Ebensperger, 1998; Janson & van Schaik, 2000; van

16 Schaik, 2000a). Of the five explanatory hypotheses put forward to explain infanticide

17 (overview e.g. in Hrdy, 1979; Hausfater & Vogel, 1982), the most pertinent has proven to be

18 the sexual selection hypothesis, which attributes infanticide to male-male competition for

19 reproduction (Hrdy, 1974). According to this hypothesis, killing of an infant results in

20 reproductive advantage for male mammals under the following conditions: 1) only unrelated

21 infants are killed; 2) premature loss of an infant enables the mother to conceive the next

22 infant sooner; 3) the males' chances of siring the next infant are high. In addition, it has been

23 argued that by killing an unrelated infant, males increase their own relative, genetic

24 representation in the population simply because they reduce the genetic representation of a

25 competing male (Hrdy, 1974; Hausfater & Vogel, 1982). While this is certainly true, the

1 magnitude of such an indirect benefit has not been explored and its importance especially in

2 relation to a reduced interbirth interval is not clear.

3 Most data for primates (van Schaik, 2000b), carnivores (Pusey & Packer, 1994) and

4 rodents (Blumstein, 2000) support the sexual selection hypothesis. They mainly refer to

5 groups containing only one breeding male called one-male groups. From time to time, this

6 male is replaced by a new male (e.g. Struhsaker, 1977; Sommer, 1988) who may attack and

7 eventually kill infants. Mothers and other group members usually defend the infant and

8 female-female coalitions are common in this context. However, male defence is considered

9 more efficient and riskier to the attacker than female defence (Hrdy, 1974; van Schaik,

10 2000b) but in one-male groups the father will no longer be around to protect his progeny.

11 Previous models (Chapman & Hausfater, 1979; Hausfater et al., 1982; Breden &

12 Hausfater, 1990) mainly referred to the best data available at that time, the records for

13 Hanuman langurs (*Semnopithecus (Presbytis) entellus*) living at three different sites in India

14 (Sugiyama, 1965; Mohnot, 1971; Hrdy, 1977). Perhaps because in these populations the one-

15 male group type predominates, the models likewise assume one-male settings. Infanticide in

16 multi-male groups was observed but considered to be less likely (e.g. Busse and Hamilton,

17 1981; Sekulic, 1983; Leland et al., 1984; Newton, 1988; van Schaik, 1996) because potential

18 male defenders will increase the costs for and reduce the success rates of attackers. The

19 chances seem smaller for an infanticidal male to sire the next infant and thus to benefit from

20 infanticide. He risks killing his own offspring particularly if mating skew is low and male

21 tenure is long.

22 It has recently been confirmed that infanticide may indeed occur in primate multi-male

23 groups (e.g. de Ruiter et al., 1994; Borries, 1997; Palombit et al., 2000; Soltis et al., 2000)

24 and that it may be in accordance with the sexual selection hypothesis (Borries et al., 1999a;

25 Crockett & Janson, 2000). Males already residing in the group were observed to defend

3

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 & 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 & Koenig, 2000; Janson & 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 & 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 infants 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.

The Model

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

1   retains the key features of whether to attack and whether to defend in the face of an attack.

2   This yields a composite evolutionarily stable strategy, which tells us how a male in either

3   position should behave, under any circumstances.

4   Infanticide may involve several unsuccessful attacks by the male (e.g. Borries, 1997;

5   Palombit et al., 2000; Soltis et al., 2000). In our model an attack is thus defined as the whole

6   period from the moment when the new male begins to attack the infant until he either gives

7   up permanently or kills it. It is further assumed that the mother and possibly some of the other

8   females try to defend the infant so that there is always some risk involved in attacking an

9   infant.

10

11   DEFINING MALE BENEFITS

12   We consider the expected reward E to either male as a function of the expected number of his

13   infants, i, which reach maturity and the total (effective) population size, y, composed of all

14   individuals in direct competition with each other as part of the same gene pool.

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

16   where R is a competition function which decreases as y increases. As the population gets

17   larger, there is more competition and thus reduced representation.

18   All benefits are given relative to those at the current population size x. An infant which

19   reaches maturity when the population size is x is worth payoff 1 to its father. Thus we set

20   $R(x) = 1$. This standardisation is possible since $R(x)$ only influences our analysis through the

21   factor I which depends upon the relative size of $R(x)$ and $R(x-1)$ only (see Table 1).

22   If there is sufficient food, so that competition over food is irrelevant and the population

23   has room to increase in numbers, then strict numbers are more important than the proportion

24   of the gene pool and so

25   $R(y) = 1$, independent of y.

1   However, if the population cannot expand as is the case for most natural populations that

2 live close to the carrying capacity, the proportion of the gene pool becomes more important

3 and $R(y)$ is proportional

4 to $\dfrac{1}{y}$ i.e. $R(y) = \dfrac{x}{y}$.

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

6 $R(y) = \varphi \dfrac{x}{y} + (1-\varphi)$

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

8

9   PARAMETERS

10 The general characteristics of the model population are given in Table 1. These parameters

11 will obviously vary according to species, dominance effects, number of females etc. It is

12 likely that:

13     $g(t)$ is a decreasing function of t, tending to 0 for large t. The younger a dependent infant

14   dies, the shorter the inter-birth interval of its mother (Altmann et al., 1977; Sommer,

15   1994; Borries, 1997);

16   the injury probabilities q_1, q_3 are relatively small. In fact, very few cases are reported for

17   primates (van Schaik, 2000b);

18     $v > q_1 + q_2$ so that the probability of the infant being killed is reduced (markedly) if the

19   father defends. Here we follow the assumption of several researchers (e.g. Altmann, 1990;

20   Newton & Dunbar, 1994; van Schaik, 1996);

21     $A_f + E_f + \alpha + \beta(t)$ is the father's total expected number of infants surviving to maturity (for the

22   new male it is $A_n + E_n$). This formula gives his lifetime reproductive success, if no

23   infanticide or injury results from the present encounter (if infanticide or injury does occur,

24   then these formulas vary according to Table 2);

1   the ratio of expected to existing offspring varies with the age of the males and $A > E$ for

2   an old male while $A < E$ for a young male;

3   a male's rank will act on the paternity probability and on the risk of injury with p being

4   small, $q_1 > q_3$ if the father is subordinate and p being large, $q_1 < q_3$ if the father is

5   dominant while p will be intermediate, $q_1 = q_3$ if there is no rank effect.

6

7   BENEFITS UNDER DIFFERENT CIRCUMSTANCES

8   In case an attack occurs and the father defends, both males are faced with a particular risk of

9   being injured. For reasons of simplicity, we assume that injury is equivalent to disappearance

10   or death of the adult male and a residual reproductive value E of zero, an extreme though

11   likely consequence in primates (e.g. Sommer, 1988). If the father is injured during defence,

12   the infant is killed, while if the new male is injured the infant survives. The lifetime

13   reproductive success of each of the two males under the different circumstances is

14   summarized in Table 2. It is composed of the number of already existing offspring A plus the

15   future offspring E, modified by the competition function R. Furthermore, if the target infant

16   survives (no or unsuccessful attack) it is added to the father's reproductive success modified

17   by its chances to survive $\alpha + \beta(t)$. If the target infant is killed an extra infant is added to either

18   male with probability equal to $g(t)$, modified by the newborn infant's probability of survival α

19   and by the probability of paternity p. Competition in the population is reduced to $R(x-1)$.

20   We now find the conditions for infanticide and infant defence, i.e. two conditions are

21   distinguished in the model population:

22   A. Condition A indicates under which circumstances it is best for the father to defend if there

23   is an attack. If A holds, this implies that the father should defend the infant whereas, if

24        $\overline{A}$ holds (A does not hold), he should not.

1 B. Condition B indicates when it is best for the new male to attack, assuming there will be

2   defence by the father. If there will be no defence then there remains only the risk of injury

3   via female defence, which for reasons of simplicity is assumed to be zero, so an attack

4   would always be best (but see below). If B holds, this implies that the new male should

5   attack the infant, whereas if $\overline{B}$ holds, he should not.

6   This argument generates three possible situations:

7 (1) $\overline{A} \Rightarrow$ new male attacks, father does not defend

8 (2) $A \bigcap B \Rightarrow$ new male attacks, father defends

9 (3) $A \bigcap \overline{B} \Rightarrow$ new male does not attack

10   Weighting the various possible rewards from Table 2 by the probability of their

11 occurrence, the reward to the father is,

12 $q_1 A_f R(x\text{-}1)+q_2[E_f+A_f+g(t)p\alpha]R(x\text{-}1)+q_3(E_f+A_f+\alpha+\beta(t))R(x)+(1\text{-}q_1\text{-}q_2\text{-}q_3)(E_f+A_f+\alpha+\beta(t))R(x)$

13 if he defends, and $v\,[E_f+A_f+g(t)p\alpha]R(x\text{-}1)+(1\text{-}v)(E_f+A_f+\alpha+\beta(t))R(x)$ if he does not. A occurs if

14 the benefit to the father is greater if he defends than if he does not, i.e.

15 $q_1 A_f R(x\text{-}1)+q_2[E_f+A_f+g(t)p\alpha]R(x\text{-}1)+q_3(E_f+A_f+\alpha+\beta(t))R(x)+(1\text{-}q_1\text{-}q_2\text{-}q_3)(E_f+A_f+\alpha+\beta(t))R(x) >$

16 $v\,[E_f+A_f+g(t)p\alpha]R(x\text{-}1)+(1\text{-}v)(E_f+A_f+\alpha+\beta(t))R(x)$

17 $\Rightarrow (E_f+A_f+\alpha+\beta(t))[R(x)\text{-}R(x\text{-}1)](v\text{-}q_1\text{-}q_2)\text{-}(\alpha+\beta(t))R(x\text{-}1)(q_1+q_2\text{-}v)\text{-}q_1E_fR(x\text{-}1)+g(t)p\alpha R(x\text{-}1)(q_2\text{-}$

18 $v) > 0$

19 Setting $I = \dfrac{R(x-1)-R(x)}{R(x-1)}$ implies that A occurs if

20 $(E_f+A_f+\alpha+\beta(t))(v\text{-}q_1\text{-}q_2)I+g(t)p\alpha(v\text{-}q_2)\text{-}[(\alpha+\beta(t))(v\text{-}q_1\text{-}q_2)\text{-}q_1E_f] < 0$

21   B occurs if the benefit to the new male is greater if he attacks, assuming that the father

22 defends, than if he does not attack. Similarly weighting the rewards from Table 2 for the new

23 male, we obtain B if

1 $q_1(E_n+A_n+g(t)\alpha)R(x-1)+q_2(E_n+A_n+g(t)(1-p)\alpha)R(x-1)+q_3A_nR(x)+(1-q_1-q_2-q_3)(E_n+A_n)R(x) >$

2 $(E_n+A_n)R(x)$

3 $\Rightarrow (E_n+A_n)(q_1+q_2)[R(x-1)-R(x)]-q_3E_nR(x)+g(t)\alpha R(x-1)[q_1+q_2(1-p)] > 0$

4 dividing by $R(x-1) \Rightarrow [(E_n+A_n)(q_1+q_2)+q_3E_n]\,I+g(t)\alpha[q_1+q_2(1-p)]-q_3E_n > 0$

5   These inequalities indicate how the values of the different parameters influence the

6 likelihood of the new male to attack and the father to defend (Table 3). Of course, some of

7 these parameters are not independent and are heavily influenced by the dominance ranks of

8 the males. This is apparent in the following examples which illustrate some of the key

9 predictions of the model.

10   The above inequalities A and B are linear in the terms $g(t)$ and I and so these terms affect

11 the propensity for attack and defence in a straightforward way. Fixing all the above

12 parameters in the two equations (i.e. leaving them at a constant value while varying the

13 chosen ones) reveals that both attack and no defence are favoured by larger I and larger $g(t)$,

14 so that infanticide is more likely the larger these are. Since the new male's gain (through $g(t)$)

15 is largest for small values of t, males should preferentially attack young infants. Note that for

16 the father, the loss is larger for older infants (their survival rate is better) so that defence is

17 more important then. The difference in competition due to the death of a single individual (I)

18 is largest for a population low in number, with a small gene pool.

19

20 **Examples**

21 To explore the effect of male age and dominance on the occurrence of attack and defence and

22 to simulate natural scenarios for different primate species we calculate several examples. In

23 these examples the following factors are considered constant. φ is set to equal 1. The

24 population size is moderate ($x = 1000$) resulting in a value of the competition function

25     $R(y) = \dfrac{1000}{y}$ i.e. $I = \dfrac{R(999)-R(1000)}{R(999)} = 0.001$.

1   The probability of survival to maturity for newborn infants is set to $\alpha = 0.5$, a value most

2   commonly found in undisturbed primate populations (e.g. Altmann et al., 1978; Borries &

3   Koenig, 2000; Palombit et al., 2000). The probability of survival to maturity for the target

4   infant provided there is no infanticide varies with age of the infant with $\beta(t) = 0.2t$ and $t \leq 2$.

5   Note that the oldest monkey killed by a male was 18 months old and the oldest ape 21 months

6   (van Schaik, 2000b) and most monkeys terminate infancy before turning two years of age.

7   The expected number of extra births if infanticide occurs is $g(t) = 0.5 - 0.25t$ $t \leq 2$ (cf. above).

8   It is reported in Sommer (1994) that out of 110 infants exposed to a new male in single male

9   groups (so that only female defence was available), 53 were observed to be attacked of which

10   39 were killed (35% of the total, 74% of those seen to be attacked). Given that many attacks

11   go unobserved, but all fatalities are observed, 74% is likely to be a significant overestimate of

12   the success percentage. In our examples we set the probability that the target infant is killed if

13   only females defend as $\nu = 0.5$. Both males are assumed to have a similar life-time

14   reproductive success of $E_f + A_f = E_n + A_n = 5$, a likely mean value for stable primate populations

15   which usually contain more adult females than adult males. In fact the father's life-time

16   reproductive success is $A_f + E_f + \alpha + \beta(t)$ and so is a little higher than the new male's.

17   All other factors vary depending on the age and rank of the males. Age affects the

18   residual reproductive value (E), while rank is assumed to affect the relative probability of

19   being injured (q_1 and q_3), the probability that the infant is killed $q_1 + q_2$ if the father defends,

20   and the reproductive skew expressed via p.

21

22   EXAMPLES 1 – MALES EVENLY MATCHED (SAME RANK)

23   Under some conditions male reproductive success does not depend on dominance (e.g.

24   Shively & Smith, 1985; Berard et al., 1993; Paul & Kuester, 1996). Even though most of

25   these paternity data stem from captive or semi-free ranging primates, in some societies male

1   dominance rank seems of little importance (Strier, 1994). Similar rank implies identical risk

2   of injury and identical paternity probability. Hence, $q_1 = q_3 = 0.02$, $q_2 = 0.38$ (so $q_1 + q_2 = 0.4$),

3    $p = 0.5$. For these examples, the two conditions thus reduce to A occurs if

4    $0.1(5.5+0.2t)*0.001+0.03(0.5-0.25t)-[0.1(0.5+0.2t)-0.02E_f]= -0.03445+0.02\ E_f\ -0.02748t < 0$

5   and B occurs if

6    $[2+0.02E_n]*0.001+0.105(0.5-0.25t)-0.02E_n =0.0545-0.01998\ E_n\ -0.02625t > 0$

7   Because there is no *a priori* justification for male age we explore the effect of age of the two

8   males on defence and attack patterns for all four extreme combinations:

9   (i) Both males are young, $E_f = E_n = 4$;

10   then *A*: $-0.03445+0.02*4-0.02748t < 0 \Rightarrow t > 1.66$

11   *B*: $0.0545-0.01998*4-0.02625t > 0 \Rightarrow B$ does not hold

12   i.e. $t < 1.66$ new male attacks, father does not defend; $t > 1.66$ no attack.

13   (ii) Both males are old, $E_f = E_n = 1$; then *A* always holds, *B* holds if $t < 1.32$

14   i.e. $t < 1.32$ new male attacks, father defends; $t > 1.32$ no attack.

15   (iii) The father is old, the new male young, $E_f = 1$, $E_n = 4$; then *A* always holds, *B* does not

16   hold i.e. there is no attack.

17   (iv) The father is young, the new male old, $E_f = 4$, $E_n = 1$; then *A* holds if $t > 1.66$,

18   *B* holds if $t < 1.32$ i.e. $t < 1.66$ new male attacks, father does not defend; $t > 1.66$ no attack.

19   These examples show that the defence of fathers depends on their residual reproductive

20   value. If it is low, the value of the target infant might become decisive. In other words older

21   fathers are more likely to defend young infants than younger fathers. The latter may only

22   defend old infants. Male attack similarly depends on the residual reproductive value, i.e. *B*

23   does not hold for young males and they would only attack, if fathers do not defend. In

24   contrast, old males may attack despite defence of (old) fathers.

25

1   EXAMPLES 2 – MALES NOT EVENLY MATCHED (DIFFERENCE IN RANK)

2   Most studies of wild primates have shown that male reproductive success depends on

3   dominance rank with the highest ranking male, the alpha male being most successful (e.g. de

4   Ruiter et al., 1994; Bercovitch & Nürnberg, 1997; Gust et al., 1998; Launhardt et al., 2001).

5   These societies may differ, however, in male migration pattern. In some populations males in

6   their prime age immigrate and take over the alpha position from older males (Borries, 2000;

7   Palombit et al., 2000). Depending on the turn-over rate for the alpha position, the difference

8   in age might only be small. In other cases young males enter the hierarchy at the bottom

9   (Sprague et al., 1998; van Noordwijk & van Schaik, 2001) or older males frequently change

10   groups (Alberts & Altmann, 1995; Borries, 2000). Unequal dominance rank is likely to

11   translate into different risks of injury with the dominant male facing a smaller risk. The

12   reproductive skew (p) will also be altered. In addition, the probability that the infant is killed

13   with no male injured (q_2) may change, and with it the overall probability that the infant is

14   killed in an attack (q_1+q_2). However, since this sum mainly affects the results through (v-q_1-

15   q_2), we shall not alter it for simplicity. Even though other scenarios may be possible, the

16   examples below are the most likely scenarios among nonhuman primates. In each case we

17   return to the original conditions A and B to find the optimal behaviour.

18   *Examples 2a - Father Subordinate.* (i) The father is subordinate and old, the new male is

19   dominant and young, with $q_1 = 0.03$, $q_3 = 0.01$, $q_2 = 0.37$ (so $q_1+q_2 = 0.4$), $p = 0.2$, $E_f = 1$, $E_n =$

20   4; then A always holds, B holds if $t < 1.07$ i.e. $t < 1.07$ new male attacks, father defends; $t >$

21   1.07 no attack.

22   (ii) The father is subordinate but only slightly older than the new male who is dominant and

23   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

24   holds if $t > 0.73$, B holds if $t < 1.07$ i.e. $t < 0.73$ new male attacks, father does not defend;

25    $0.73 < t < 1.07$ 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.

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

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

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

2   The largest plausible value of I is $\dfrac{1}{x}$, and it may well be a lot smaller. Thus, for a

3 population of 1,000 individuals, $I < 0.001$. The reduced interbirth interval $g(t)$ typically may

4 range from 0 to 0.5 (cf. Struhsaker & Leland, 1987; van Schaik, 2000b). When the reduced

5 interbirth interval is an important factor, the interference term is dwarfed by it, and so at most

6 adds a small secondary benefit. For example in Example 1(i), in the case of a newborn infant,

7 the numerical value in the equation for conditions A of the term including I is 0.00085 and the

8 corresponding value for the term including $g(t)$ is 0.015. Similarly, the contributions of the

9 terms including I and $g(t)$ in the equation for condition B are 0.00328 and 0.0525

10 respectively. In each case the contribution of reduced interbirth interval is 16 times higher

11 than the competition term. In the other examples the difference is even more extreme. This

12 tendency is even stronger for larger and probably more natural population sizes. As long as

13 there is a noticeable advantage gained via a reduction in the subsequent interbirth interval

14 indirect benefits seem to be of minor importance.

15   To explore the effect of mere indirect benefits we consider $g(t) \equiv 0$ i.e. the interbirth

16 interval is not reduced by infanticide.

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

18   B becomes $[(E_n + A_n)(q_1 + q_2) + q_3 E_n]I - q_3 E_n > 0$

19   The father will only not defend (A not satisfied) if the 2nd term is negative, which occurs

20 only if the father runs a large risk of injury in defence without giving much extra protection

21 to what the female coalition would. So it is very likely that the father defends the infant. B

22 will only occur if the new male's risk of injury is extremely (unfeasibly) small. As soon as an

23 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.

Conclusions

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.

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

1 young infants because they will not be defended by the father. For subordinate fathers

2 defence depends on their residual reproductive value. A low value renders defence more

3 likely.

4 In general any factor which has an effect on the values of our parameters will influence

5 the optimal behaviour. A new male attaining top dominance right after immigration is typical

6 for chacma baboons (*Papio ursinus*) at the Moremi Game Reserve, Botswana or Hanuman

7 langurs (*Semnopithecus entellus*) of Ramnagar, Nepal (Borries, 2000; Palombit et al., 2000).

8 Consequently infanticide is common and its impact on infant mortality is high.

9 The situation should be markedly different for new males immigrating as subordinates.

10 Their decision to attack should entirely depend on the father's behaviour and they will only

11 attack if he does not defend which holds true for young fathers with young infants whereas

12 old fathers will always defend. In several primate multi-male groups it is common for

13 immigrant males to attain subordinate ranks (e.g. *Macaca fuscata*, Sprague et al., 1998;

14 *Macaca fascicularis*, van Noordwijk & van Schaik, 2001). They are confronted with

15 dominant and usually older resident males, circumstances for which no infanticide is

16 predicted. And indeed, infanticide seems to be rare in these species. The reported cases of

17 males attacking infants all happened under exceptional circumstances that seem to fit the

18 predictions, after the four highest-ranking males (the most likely fathers) had left the group

19 (Soltis et al., 2000) and after the attackers had rapidly risen in rank (de Ruiter et al., 1994).

20 However, it is currently not known whether young fathers will indeed not defend very young

21 infants.

22 These examples suggest that the observed variation of infanticide in primate multi-male

23 groups may be explained by differences in male migration pattern and the resulting

24 differences in age and dominance rank of competing males.

25

2   Male benefits derived from infanticide are mainly influenced by a direct reproductive

3   advantage attained via the prospect of siring an extra infant. The conditions under which the

4   evolutionarily stable strategy would indicate that infanticide would occur even if it renders

5   only an indirect advantage are rather narrowly defined: the attacker's risk has to be very

6   small. Perhaps the few observed cases when males attacked infants residing in neighbouring

7   groups fit this scenario (e.g. Borries, 1997). The recently described case of infanticide in

8   patas monkey (*Erythrocebus patas*, Enstam et al., 2002) might be another example for

9   exceptional circumstances. A single male in a group of females killed an infant although the

10 subsequent interbirth interval was not shortened in this seasonally and annually breeding

11 species. It is likely that patas males, when alone in a group of females, face a very low risk of

12 being injured indicated by a rather high general canine dimorphism index (GCDI) and one of

13 the highest body weight dimorphisms amongst anthropoid primates (Plavcan and & Schaik,

14 1992, 1997). Mere indirect advantages might, furthermore, be sufficient if the population size

15 is very small (e.g. in populations close to extinction). It is, however, not clear whether this

16 situation occurs in nature.

17   More generally, in multi-male groups with little prospect of direct benefits, a male is

18 expected to refrain from attack if he would risk being injured. Since females almost always

19 defend and defence by fathers is very likely (if their costs are small or moderate), new

20 immigrant males will not attack. Mere indirect benefits are most probably not sufficient to

21 explain the evolution of infanticide by males.

22

23   PERSPECTIVES

24 So far we have restricted our exploration to the smallest multi-male group possible, a single

25 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 & 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.

References

ALBERTS,S.C.&ALTMANN,J. (1995). Balancing costs and opportunities: dispersal in male

  baboons. *American Naturalist* **145**, 279-306.

ALTMANN,J.(1990). Primate males go where the females are. *Animal Behaviour* **39**, 193-

  194.

ALTMANN,J.,ALTMANN,S.A.&HAUSFATER,G.(1978). Primate infant's effects on

  mother's future reproduction. *Science* **201**, 1028-1030.

ALTMANN,J.,ALTMANN,S.A.,HAUSFATER,G.&MCCUSKEY,S.(1977). Life history of

  yellow baboons: Physical development, reproductive parameters, and infant mortality.

  Primates **18**, 315-330.

1   BERARD,J.D.,NUERNBERG,P.,EPPLEN,J.T.&SCHMIDTKE,J. (1993). Male rank,

2   reproductive behavior, and reproductive success in free-ranging rhesus macaques.

3   *Primates* **34**, 481-489.

4   BERCOVITCH,F.B.&NUERNBERG,P.(1997). Genetic determination of paternity and

5   variation in male reproductive success in two populations of rhesus macaques.

6   *Electrophoresis* **18**, 1701-1705.

7   BLUMSTEIN,D.T.(2000). The evolution of infanticide in rodents: a comparative analysis.

8   In: *Infanticide by Males and its Implications* (Ed. by C. P. van Schaik & C. H. Janson),

9   pp. 178-197. Cambridge: Cambridge University Press.

10   BORRIES,C.(1997). Infanticide in seasonally breeding multimale groups of Hanuman

11   langurs (*Presbytis entellus*) in Ramnagar (South Nepal). *Behavioral Ecology and*

12   *Sociobiology* **41**, 139-150.

13   BORRIES,C.(2000). Male dispersal and mating season influxes in Hanuman langurs living in

14   multi-male groups. In: *Primate Males: Causes and Consequences of Variation in Group*

15   *Composition* (Ed. by P. M. Kappeler), pp. 146-158. Cambridge: Cambridge University

16   Press.

17   BORRIES,C.&KOENIG,A.(2000). Infanticide in hanuman langurs: social organization, male

18   migration, and weaning age. In: *Infanticide by Males and its Implications* (Ed. by C. P.

19   van Schaik & C. H. Janson), pp. 99-122. Cambridge: Cambridge University Press.

20   BORRIES,C.,LAUNHARDT,K.,EPPLEN,C.,EPPLEN,J.T.&WINKLER,P.(1999a. DNA

21   analyses support the hypothesis that infanticide is adaptive in langur monkeys.

22   *Proceedings of the Royal Society of London B, Biological Sciences*, **266**, 901-904.

23   BORRIES,C.,LAUNHARDT,K.,EPPLEN,C.,EPPLEN,J.T.&WINKLER,P.(1999b*).* Males as

24   infant protectors in Hanuman langurs (*Presbytis entellus*) living in multimale groups -

defence pattern, paternity and sexual behaviour. *Behavioral Ecology and Sociobiology* **46**, 350-356.

BREDEN,F.&HAUSFATER,G.(1990). Selection within and between social groups for infanticide. *American Naturalist* **136**, 673-688.

BUSSE,C.&HAMILTON III.,W.J.(1981). Infant carrying by male chacma baboons. *Science* **212**, 1281-1283.

CHAPMAN,M.&HAUSFATER,G.(1979). The reproductive consequences of infanticide in langurs: a mathematical model. *Behavioral Ecology and* Sociobiology **5**, 227-240.

CROCKETT,C.M.&JANSON,C.H.(2000). Infanticide in red howlers: female group size, male membership, and a possible link to folivory. In: *Infanticide by Males and its Implications* (Ed. by C. P. van Schaik & C. H. Janson), pp. 75-94. Cambridge: Cambridge University Press.

DE RUITER,J.R.,VAN HOOFF,J.A.R.A.M.&SCHEFFRAHN,W.(1994). Social and genetic aspects of paternity in wild long-tailed macaques (*Macaca fascicularis*). *Behaviour* **129**, 203-224.

EBENSPERGER,L.A.(1998). Strategies and counterstrategies to infanticide in mammals. *Biological Reviews* **73**, 321-346.

ENSTAM,K.L.,ISBELL,L.A.&DE MAAR,T.W.(2002). Male demography, female mating behavior, and infanticide in wild patas monkeys (*Erythrocebus patas*). *International Journal of Primatology* **23**, 85-104.

FISHER,R.A.(1930). *The Genetical Theory of Natural Selection*. Oxford: Clarendon.

GUST,D.A.,MCCASTER,T.,GORDON,T.P.,GERGITS,W.F.,CASNA,N.J.&MCCLURE,H.M.(1998). Paternity in sooty mangabeys. *International Journal of Primatology* **19**, 83-94.

1   HAUSFATER,G.,AREF,S.&CAIRNS,S.J.(1982). Infanticide as an alternative male

2   reproductive strategy in langurs: a mathematical model. *Journal of theoretical Biology*

3   **94**, 391-412.

4   HAUSFATER,G.&HRDY,S.B.(1984). Eds. *Infanticide: Comparative and Evolutionary*

5   *Perspectives*. New York: Aldine.

6   HAUSFATER,G.&VOGEL,C.(1982). Infanticide in langur monkeys (genus *Presbytis*):

7   recent research and a review of hypotheses. In: *Advanced Views in Primate Biology* (Ed.

8   by A. B. Chiarelli & R. S. Corruccini), pp. 160-176. Berlin: Springer.

9   HRDY,S.B.(1974). Male-male competition and infanticide among the langurs (*Presbytis*

10   *entellus*) of Abu, Rajasthan. *Folia Primatologica* **22**, 19-58.

11   HRDY,S.B.(1977). *The Langurs of Abu: Female and Male Strategies of Reproduction*.

12   Cambridge: Harvard University Press.

13   HRDY,S.B.(1979). Infanticide among animals: a review, classification, and examination of

14   the implications for the reproductive strategies of females. *Ethology and Sociobiology* **1**,

15   13-40.

16   JANSON,C.H.&VAN SCHAIK,C.P.(2000). The behavioral ecology of infanticide by males.

17   In: *Infanticide by Males and its Implications* (Ed. by C. P. van Schaik & C. H. Janson),

18   pp. 469-494. Cambridge: Cambridge University Press.

19   LAUNHARDT,K.,BORRIES,C.,HARDT,C.,EPPLEN,J.T.,&WINKLER,P.(2001). Paternity

20   analysis of alternative male reproductive routes among the langurs (*Semnopithecus*

21   *entellus*) of Ramnagar. *Animal Behaviour* **61**, 53-64.

22   LELAND,L.,STRUHSAKER,T.T.&BUTYNSKI,T.M.(1984). Infanticide by adult males in

23   three primate species of Kibale forest, Uganda: a test of hypotheses. In: *Infanticide:*

24   *Comparative and Evolutionary Perspectives* (Ed. by G. Hausfater & S. B. Hrdy), pp.

25   151-172. New York: Aldine.

MOHNOT,S.M.(1971). Some aspects of social changes and infant-killing in the Hanuman langur, *Presbytis entellus* (Primates: Cercopithecidae), in western India. *Mammalia* **35**, 175-198.

NEWTON,P.N.(1988). The variable social organization of Hanuman langurs (*Presbytis entellus*), Infanticide, and the monopolization of females. *International Journal of Primatology* **9**, 59-77.

NEWTON,P.N.&DUNBAR,R.I.M.(1994). Colobine monkey society. In: *Colobine Monkeys: Their Ecology, Behaviour and Evolution* (Ed. by A. G. Davies & J. F. Oates), pp. 311-346. Cambridge: Cambridge University Press.

PALOMBIT,R.A.,CHENEY,D.L.,FISCHER,J.,JOHNSON,S.,RENDALL,D.,SEYFARTH,R.M.&SILK,J.B.(2000). Male infanticide and defense of infants in chacma baboons. In: *Infanticide by Males and its Implications* (Ed. by C. P. van Schaik & C. H. Janson), pp. 123-152. Cambridge: Cambridge University Press.

PARMIGIANI,S.&VOM SAAL,F.S.(1994). Eds. *Infanticide and Parental Care*. Chur: Harwood Academic Publishers.

PAUL,A.&KUESTER,J.(1996). Differential reproduction in male and female Barbary macaques. In: *Evolution and Ecology of Macaque Societies* (Ed. by J. E. Fa & D. G. Lindburg), pp. 293-317. Cambridge: Cambridge University Press.

PLAVCAN,J.M.&VAN SCHAIK,C.P.(1992.) Intrasexual competition and canine dimorphism in anthropoid primates. *American Journal of Physical Anthropology* **87**, 461-477.

PLAVCAN,J.M.&VAN SCHAIK,C.P.(1997). Intrasexual competition and body weight dimorphism in anthropoid primates. *American Journal of Physical Anthropology* **103**, 37-68.

POPE,T.R.(2000). The evolution of male philopatry in neotropical primates. In: *Primate Males: Causes and Consequences of Variation in Group Composition* (Ed. by P. M. Kappeler), pp. 219-235. Cambridge: Cambridge University Press.

PUSEY,A.&PACKER,C.(1994). Infanticide in lions: consequences and counterstrategies. In: *Infanticide and Parental Care* (Ed. by S. Parmigiani & F. S. vom Saal), pp. 277-299. Chur: Harwood Academic Publishers.

SEKULIC,R.(1983). Male relationships and infant death in red howler monkeys (*Alouatta seniculus*). *Zeitschrift für Tierpsychologie* **61**, 185-202.

SELTEN,R.(1983). Evolutionary stability in extensive 2-person games. *Mathematical Social Sciences* **5**, 269-363.

SHIVELY,C.&SMITH,D.G.(1985). Social status and reproductive success of male *Macaca fascicularis*. *American Journal of Primatology* **9**, 129-135.

SOLTIS,J.,THOMSEN,R.,MATSUBAYASHI,K.&TAKENAKA,O.(2000). Infanticide by resident males and female counter-strategies in wild Japanese macaques (*Macaca fuscata*). *Behavioral Ecology and Sociobiology* **48**, 195-202.

SOMMER,V.(1988). Male competition and coalitions in langurs (*Presbytis entellus*) at Jodhpur, Rajasthan, India. *Human Evolution* **3**, 261-278.

SOMMER,V.(1994). Infanticide among the langurs of Jodhpur: testing the sexual selection hypothesis with a long-termed record. In: *Infanticide and Parental Care* (Ed. by S. Parmigiani & F. S. vom Saal), pp. 155-198. Chur: Harwood Academic Publishers.

SPRAGUE,D.S.,SUZUKI,S.,TAKAHASHI,H.&SATO,S.(1998). Male life history in natural populations of Japanese macaques: migration, dominance rank, and troop participation of males in two habitats. *Primates* **39**, 351-363.

STRIER,K.B.(1994). Brotherhood among atelins: kinship, affiliation, and competition. *Behaviour*, **130** 151-167.

1   STRUHSAKER,T.T.(1977). Infanticide and social organization in the redtail monkey

2   (*Cercopithecus ascanius schmidti*) in the Kibale Forest, Uganda. *Zeitschrift für*

3   *Tierpsychologie* **45**, 75-84.

4   STRUHSAKER,T.T.&LELAND,L.(1987). Colobines: infanticide by adult males. In: *Primate*

5   *Societies* (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T.

6   Struhsaker), pp. 83-97. Chicago: University of Chicago Press.

7   SUGIYAMA,Y.(1965). On the social change of Hanuman langurs (*Presbytis entellus*) in

8   their natural condition. *Primates* **6**, 381-418.

9   VAN NOORDWIJK,M.A.&VAN SCHAIK,C.P.(2001). Career moves: transfer and rank

10   challenge decisions by male long-tailed macaques. *Behaviour* **138**, 359-395.

11   VAN SCHAIK,C.P.(1996). Social evolution in primates: the role of ecological factors and

12   male behaviour. *Proceedings of the British Academy* **88**, 9-31.

13   VAN SCHAIK,C.P.(2000*a)*. Vulnerability to infanticide by males: patterns among mammals.

14   In: *Infanticide by Males and its Implications* (Ed. by C. P. van Schaik & C. H. Janson),

15   pp. 61-71. Cambridge: Cambridge University Press.

16   VAN SCHAIK,C.P.(2000*b)*. Infanticide by male primates: the sexual selection hypothesis

17   revisited. In: *Infanticide by Males and its Implications* (Ed. by C. P. van Schaik & C. H.

18   Janson), pp. 27-60. Cambridge: Cambridge University Press.

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 $t \leq 2$ years as occurs in Hanuman langurs (Borries 1997), then $$g(t) = \frac{1}{2.4}(1.2\text{-}0.6t) = 0.5\text{-}0.25t \quad t \leq 2$$
$I = \dfrac{R(x-1) - R(x)}{R(x-1)}$	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	$A_fR(x-1)$	$[A_n+E_n+g(t)\alpha]R(x-1)$	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	$(A_f+E_f+\alpha+\beta(t))R(x)$	$A_nR(x)$	q_3
Yes	Yes	No	No	$(A_f+E_f+\alpha+\beta(t))R(x)$	$(A_n+E_n)R(x)$	$1-q_1-q_2-q_3$

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	
ν	large	
q_1	small	large
q_2		large
q_3		small
$\nu\text{-}q_1\text{-}q_2$	large	
p	small	small ($1\text{-}p$ = 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. $\nu\text{-}q_1\text{-}q_2$ the probability that the target infant survives is increased by father's defence.