



The willing cuckold: optimal paternity allocation, infanticide and male reproductive strategies in mammals

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Infanticide is believed to be an adaptive strategy in many mammalian taxa. A number of authors have modelled aspects of infanticide and its potential impact on social systems, but limited attention has been paid to identifying the full range of conditions under which infanticide should be favoured or the variety of potential effects that infanticide may have on male mating strategies. While most authors focus on infanticide by new male immigrants, natural selection should favour infanticide under a wider range of conditions, including sometimes by potential fathers. Here we model male decisions about whether to commit infanticide and explore how infanticide risk may affect optimal male mating strategies. Infanticide risk coupled with imperfect infanticide protection in a population creates a fitness landscape with two adaptive peaks, one representing complete paternity certainty and the other representing a compromise between maximizing paternity and minimizing infanticide risk. Which of these adaptive peaks represents the fitness-maximizing global optimum depends on a population's socioecology and characteristics of the male. In many ecological contexts, males may adaptively reduce their paternity probability to reduce the risk of infanticide. Explicit consideration of this possibility may enhance our understanding of the dynamics of mammalian intrasexual and intersexual competition in a number of ways.

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Many researchers have commented on the adaptive potential of infanticide by males in mammals, including primates, social carnivores, rodents, cetaceans and ungulates (e.g. Hrdy 1977, 1979; Packer & Pusey 1984; Ebensperger 1998; Lewison 1998; Patterson et al. 1998; Blumstein 2000; van Schaik 2000a; Harcourt & Stewart 2008). For many species, authors have claimed that the evidence best supports what they term the 'sexual selection hypothesis', which posits that a male will kill an unrelated infant to increase his opportunity to successfully sire subsequent offspring with that infant's mother (Hrdy 1974). Much of this research has focused specifically on the reduction of females' interbirth intervals due to infanticide, which can cause more rapid return to oestrus, as in primates, or more rapid embryonic implantation, as in murine rodents (Hrdy 1977; Elwood & Ostermeyer 1984). Alternative mechanisms by which the reproductive success of infanticidal males may be augmented include increasing the number of offspring in the next litter or raising the probability that subsequent

offspring will survive (Elwood 1994; Ebensperger & Blumstein 2007). Researchers commonly assume that males should only kill infants that they could not have fathered. Under this view, infanticide committed by potential sires refutes the adaptive hypothesis or is generally considered pathological (e.g. Blumstein 2000; van Schaik 2000b; Knopff et al. 2004; Murray et al. 2007; Ebensperger & Blumstein 2007; Feh & Munkhtuya 2008). Beyond this basic framework, relatively little research has focused on identifying the exact conditions that favour infanticide under the assumptions of the sexual selection hypothesis (but see van Schaik 2000b; Broom et al. 2004).

While various female counterstrategies against infanticide by males, including paternity confusion, have been widely discussed (Hrdy 1979; Packer & Pusey 1984; Elwood et al. 1990; Agrell et al. 1998; van Schaik et al. 2000; Ebensperger & Blumstein 2007), the discussion of male counterstrategies largely has been limited to territoriality and the direct protection of infants by potential fathers (e.g. Dunbar 2000; Ebensperger & Blumstein 2007; but see Harcourt & Stewart 2008). Other potential male counterstrategies against infanticide by other males have received little attention. For example, here we argue that natural selection would, in certain situations, favour males that concede some probability of paternity to other males to reduce the risk of infanticide. Current models

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generally address the optimal strategy for a single male. In these models, paternity is implicitly used as a direct proxy for male reproductive success, and males are assumed to always favour higher paternity probability (e.g. Dunbar 2000). However, male strategies evolve in a social milieu in which all males are attempting to maximize their fitness. Thus, models that explicitly consider male behaviour within populations in which multiple males are concurrently attempting to use optimal strategies should more realistically describe the true evolutionary dynamics under which male mating strategies evolve. Mating strategies in the face of infanticidal threat present a particularly complex situation as mating and mate-guarding effort decisions facing the male must be optimized with respect to the expected behaviour of other males at a future time, after the offspring's birth. Thus uncertainty exists with respect to other males' states when the offspring will be vulnerable to their attacks.

Here we present a theoretical investigation of a range of conditions under which infanticide may provide a fitness advantage to males, and discuss how infanticide risk may shape male mating strategies. Specifically, we use simple mathematical models to identify the conditions under which males should commit infanticide and then explore how males should allocate mating effort (including mate-guarding effort) in the face of that infanticide risk. We do not attempt to explicitly model possible mechanisms underlying fine-tuned behaviour; however, we do cite relevant studies demonstrating mechanisms possibly underlying behaviour conforming to our model where appropriate. We also note that fine-tuned, context-specific mating and parenting behaviour has been observed in a range of mammals in both wild and captive contexts (e.g. Blumstein 2000; Stumpf & Boesch 2005). While we have restricted our discussion to infanticide by male mammals, the model itself could be extended to other animals that provide parental care and potentially show variable birth timing, such as some bird and insect species (Schneider & Lubin 1997; Veiga 2000). In addition, we acknowledge that while our models describe optimal male strategies within the parameters included in our models, realized male strategies will rarely achieve these optima for a variety of reasons.

WHEN IS INFANTICIDE BY MALES ADAPTIVE?

Infanticide has commonly been recognized as a strategy that a male may use upon taking over a new group or territory in polygynous species, or newly pairing with a female in monogamous species. Under these conditions, the male has no probability of having sired the infants he encounters at that time, and by killing existing infants he reduces the amount of time he will have to wait for females to bear his offspring (e.g. primates: Hrdy 1979; carnivores: Packer & Pusey 1984; rodents: Wolff & Cicirello 1989; ungulates: Duncan 1982; see Fig. 1). However, it has been noted that infanticide may be an adaptive strategy in other situations as well (van Schaik 2000b; Broom et al. 2004). For example, infanticide is likely to be adaptive when a male in a multimale group has rapidly risen or expects to rise soon in rank or when a high-ranking individual was sick, incapacitated or absent when an infant was conceived. This could explain infanticide seen within groups in male-philopatric species, such as chimpanzees, *Pan troglodytes*, even when the infanticidal male could be the infant's father (Hamai et al. 1992; Murray et al. 2007). Infanticide committed against females from neighbouring territories, such as seen in male house mice, *Mus musculus*, and savanna baboons, *Papio anubis*, may also be adaptive, but only if the male may have the chance to subsequently mate the female (Collins et al. 1984; Manning et al. 1995).

Assuming a male suffers no significant costs attempting infanticide, such as injury from male or female defence (Elwood et al. 1990), or subsequent female refusal of the infanticidal male (Harcourt & Stewart 2008), infanticide is an adaptive strategy when a male's paternity probability would be greater for the next infant that a female has than for her current infant, assuming infanticide decreases a female's interbirth interval (see Fig. 1). Note that other possible adaptive mechanisms mentioned above, such as increased litter size, increased probability of having a litter in the following year or enhanced survivorship of subsequent offspring, could also be incorporated into this model framework with small modifications. Finally, we recognize that infanticide may have other adaptive functions in females and males, such as providing direct nutritional benefits or reducing competition, that are not covered

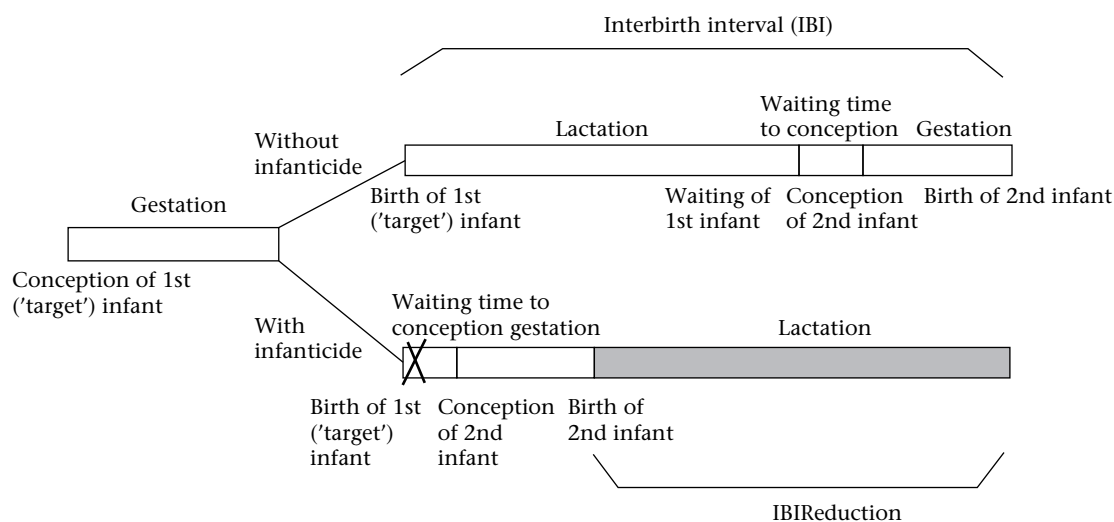


Figure 1. Parental investment in two infants during one interbirth interval (IBI_{full}) with and without infanticide. Here we refer to IBI_{full} as the full expected interbirth period following the birth of the first infant if that infant were to survive. The top timeline represents the situation where infanticide does not occur, while the bottom timeline includes an infanticide (marked by the 'X'). Without infanticide, at the end of the IBI_{full} , there is one weaned infant and a second, newborn infant. With infanticide, the first infant is dead, leaving only the second infant, which is of age IBI_{full} minus $IBIReduction$, where $IBIReduction$ equals the sum of 'age of first infant at infanticide', 'waiting time to conception' and 'gestation time'. The grey area represents this reduction in IBI_{full} (' $IBIReduction$ ') because of the infanticide. $IBIReduction/IBI_{full}$ is directly proportional to a male's genetic payoff for committing infanticide. Gestation periods are the same in the two scenarios, while the waiting time to conception may differ between scenarios.

by this model and that would be more likely to occur in animals with seasonal reproduction; however, the sexual selection hypothesis covered by this model seems well supported in many taxa (van Schaik 2000b; Ebensperger & Blumstein 2007).

In the absence of infanticide, after one interbirth interval (IBI), a male obtains a genetic 'payoff' proportional to the expected proportion of his genes in the offspring born at the start of that IBI. Hereafter, we use the term IBI_{full} to refer to the potential full IBI that the female would experience if her offspring survived, while we use IBI_{actual} to refer to the actual interbirth interval experienced by the female; in the case of no infanticide or external mortality, IBI_{full} is equivalent to IBI_{actual} . For simplicity, we set the payoff to the male for his own offspring at 1 and the payoff for any other male's offspring at 0. (We explore later how potential inclusive fitness benefits due to relatedness among males within a group would affect this system). However, in any given case, a potential sire does not know whether an offspring is his (we consider phenotypic signs of genetic relatedness later), so his estimated genetic payoff would be his estimation of his own paternity probability, $P(p^0)$, weighted by the payoff for having an offspring, in this case 1 (see Table 1 for a definition of terms). Thus, at the end of one IBI_{full} , in the absence of infanticide, the male's estimated payoff is merely his (presumably subconscious) estimation of his paternity probability in the first offspring (plus some discounted value based on his paternity probability of the newborn second offspring, but as gestation of the second offspring occurs within the IBI_{full} whether or not there is infanticide, this cancels out; see below). Note here that we do not assume a specific paternity estimation mental faculty but merely some mechanism yielding behaviour broadly consistent with such a faculty; for example, copulation with a female reduces a male house mouse's infanticide response to her offspring, while copulation coupled with continued proximity to that female during her receptive period reduces a male's infanticide response further still (Elwood 1985, 1986).

If infanticide occurs, a male will receive no genetic payoff from the dead, first offspring. However, the male will receive a partial payoff for the female's next offspring (the second offspring) during the remainder of the expected IBI_{full} that would have occurred if the first offspring had survived, assuming the female's realized IBI, IBI_{actual} , is reduced. This payoff represents the portion of the IBI_{full} that the female can devote to her next conceived offspring during the dead offspring's IBI_{full} , subtracting the gestation time that would

have occurred within the first offspring's IBI_{full} regardless (IBIReduction/ IBI_{full} ; see Fig. 1). This payoff will be multiplied by the male's expected probability of paternity of the second offspring, $E(p_i)$, which is determined by his expected state, i , when it is conceived. For many species, the male's state can be considered to be his rank in the dominance hierarchy or his residence status. Thus, $E(p_i) \times IBIReduction/IBI_{full}$ represents the full payoff to an infanticidal male because after the IBI_{full} period following the birth of the first offspring, the female will be investing in the second offspring regardless of whether infanticide occurred (and the gestation period for the second offspring will occur within the IBI_{full} after the first offspring's birth in either case). The expected probability of paternity of the next offspring is determined by his expected state when that offspring is conceived, hence, the subscript i in inequality (1). Thus, a male should commit infanticide when:

$$E(p_i) \frac{IBIReduction}{IBI_{full}} > P(p^0) \quad (1)$$

This inequality yields several plausible predictions. First, if $P(p^0)$, the probability of having sired the current (first) infant, is 0, then infanticide would always be favoured whenever there was a reduction in the interbirth interval, IBI_{actual} , following infanticide and the infanticidal male could potentially mate with the female when she is next in oestrus, assuming the costs of committing infanticide are negligible (if necessary, such costs could be subtracted from the left side of inequality (1) and that the male accrues no other benefits from the current infant (such as indirect fitness benefits or benefits related to larger group size). This suggests infanticide may be adaptive in a wider range of circumstances than is commonly recognized (van Schaik 2000b) and comports with observations of infanticide by lower-ranking immigrant males in some species such as hanuman langurs, *Semnopithecus entellus* (Borries & Koenig 2000) and some house mice (vom Saal & Howard 1982; Perrigo et al. 1989). Second, if ranks are relatively stable and are positively correlated with paternity probability, then high-ranking males would have more incentive to commit infanticide as long as they are unlikely to be related to the target infant. This model prediction agrees with current theory (van Schaik 2000b).

As noted above, for nonfather males (those for which $P(p^0) = 0$), inequality (1) is always true whenever killing an infant would reduce the interbirth interval of the infant's mother, IBI_{actual} , assuming the infanticidal male could mate with the female in the future (i.e. $E(p_i) > 0$). For possible sires (those with $P(p^0) > 0$), fitness will be maximized by either killing the infant or protecting it, depending on the infant's age. One can find the point in an infant's life span at which males should switch between these two tactics by rearranging terms in inequality (1). Males should switch from being infanticidal to being protective when:

$$IBIReduction \leq \frac{P(p^0)IBI_{full}}{E(p_i)} \quad (2)$$

As $IBIReduction$ roughly equals the remaining period of lactation, it decreases as infant age increases. Using this logic, resident, possible sires (males with $P(p^0) > 0$) would generally benefit only from killing very young infants (e.g. the victims of intragroup chimpanzee infanticides, which are on average less than 6 months old, while chimpanzees' average age at weaning is 4 years; Harvey & Clutton-Brock 1985; Murray et al. 2007).

Separating the interbirth interval, IBI_{full} , into gestation and lactation, we can determine the conditions under which a resident male (i.e. one present when a female conceived her offspring) would benefit from committing infanticide immediately following the infant's birth. This approach ignores the waiting time to conception, but this omission has little effect on results provided that waiting

Table 1
Definition of terms used in inequalities (1–4) and (1a–3a) and equations (5–8)

Term	Definition
$P(R_i R_{cur})$	The conditional probability that a male is in state i at the time of conception of infant j given his current state, R_{cur}
$E(p_i)$	The expectation of the paternity probability of a male of state i
r^*	The expected value of the inclusive fitness benefits to the male of an infant that he does not father; can be estimated as the average relatedness among males in the group
S^j	The probability that infant j survives to adulthood
$P(p^0)$	The probability that the male fathered the first, potential 'target' infant
S^0	The probability that the first infant survives to adulthood if the male does not kill it
M	The number of possible states; if estimating state as rank, the number of males in the group
j^*	Refers to the next infant conceived by a female (the second infant) after her current infant (the first infant) is killed.
IBI_{full}	The interbirth interval that would occur after the birth of the first infant if that infant were to survive
IBI_{actual}	The actual interbirth interval that the female experiences after the birth of the first infant; if the target infant dies, IBI_{actual} may be less than IBI_{full}
$IBIReduction$	The reduction of the interbirth interval, IBI_{full} , after the first infant is killed; $IBIReduction = IBI_{full} - IBI_{actual}$

time to conception is relatively short compared to the lactation period; if it is not, the waiting time could be added to both sides of the inequality. A resident male should kill a newborn infant when:

$$\text{LactationTime} > \frac{P(p^0)(\text{LactationTime} + \text{GestationTime})}{E(p_i)} \quad (3)$$

This concept is illustrated in Fig. 2, which shows that increasing the gestation:lactation ratio decreases the incentive for a male to commit infanticide. Additionally, the figure illustrates that relatedness among group males further decreases the conditions under which infanticide is adaptive (see inequality (3a)). Inequalities (1a)–(3a) below represent inequalities (1–3) with relatedness incorporated. These were derived by merely adding the expected inclusive fitness, r^* , times the probability or expectation of the probability that the focal male does not father the infant, to the direct fitness values, $P(p^0)$ and $E(p_i)$, in inequality (1), and then deriving inequalities (2a) and (3a) from inequality (1a). We note that, in practise, r^* would be difficult to measure, but it represents the proportion of a male's genes in each related male weighted by the probability that they fathered the infant. Inequalities (1a)–(3a) quantify the intuitive expectation that increases in average relatedness (r^*) will decrease the likelihood that a male should commit infanticide (Fig. 2).

$$[E(p_i) + (1 - E(p_i))r^*] \frac{\text{IBIReduction}}{\text{IBI}_{\text{full}}} > P(p^0) + [1 - P(p^0)]r^* \quad (1a)$$

$$\text{IBIReduction} \leq \frac{\left(\frac{P(p^0)}{r^*} + 1 - P(p^0)\right) \text{IBI}_{\text{full}}}{\frac{E(p_i)}{r^*} + 1 - E(p_i)} \quad (2a)$$

$$\text{LactationTime} > \frac{\left(\frac{P(p^0)}{r^*} + 1 - P(p^0)\right)(\text{LactationTime} + \text{GestationTime})}{\frac{E(p_i)}{r^*} + 1 - E(p_i)} \quad (3a)$$

As illustrated in Fig. 2, each male in a group has a certain paternity probability threshold derived from inequality (3) or (3a); only males that 'perceive' their probability of paternity for a given infant to be below that threshold should attempt infanticide, if given an opportunity. The threshold will change with the age of the infant and a number of other factors, the most important of which are the male's current rank, the degree of reproductive skew in the group and male–male relatedness within the group. Here, reproductive skew refers to the relationship between rank and reproductive success; higher skew means more of the paternity is concentrated in the top male or males. Extragroup or immigrant males are merely a special case of this general formula where $P(p^0)$ and, presumably, r^* , are 0, so that under any conditions where infanticide reduces the interbirth interval, $\text{IBI}_{\text{actual}}$, and they have a nonzero probability of siring the female's next offspring, they should commit infanticide, assuming they suffer only negligible costs by doing so. Note that these decision rules do not work on a gradient; they are thresholds below which the male is infanticidal and above which he is not. As such, these relationships are best modelled by step functions or sharply sloping logistic equations.

We note that inequality (1) is a simplified version of a more complete inequality expressing the conditions under which infanticide is adaptive. Assuming males' conditions can be expressed by a finite number of states (which in some systems could be thought of by the traditional concept of hierarchical rank, although it could also include residence status and other factors), inequality (4), below, presents a more thorough description of when infanticide is adaptive. Here, state is modelled as a Markov process where the probability that a male will have state i when infant 1 is conceived is conditioned on his current state. Summing the expected paternity probability over each state, weighted by the probability that the male is at that state when the infant is conceived, yields his paternity expectation.

$$\sum_{i=1}^M P(R_i^j | R_{\text{cur}}) E(p_i) S_i^j \frac{\text{IBIReduction}}{\text{IBI}_{\text{full}}} > P(p^0) S^0 \quad (4)$$

In species where a female's time to return to oestrus is much shorter than the duration of male tenure, however, simply using a male's expected state at the time of the next infant's conception will yield a plausible estimate of the full Bayesian probability and may be amenable to simpler psychological or physiological mechanisms upon which natural selection might act. For many mammalian taxa, this is a plausible assumption (van Schaik 2000b). One can also assume that the male and female will survive to conception time if the male commits infanticide, as adult longevity in mammals with infanticide generally far exceeds the waiting time to conception; previous researchers have often implicitly assumed this (van Schaik 2000a, b). Indeed, in species with delayed implantation, the female may have already conceived her next offspring before her current one is killed (Elwood & Ostermeyer 1984).

Furthermore, in inequality (4), infants' values to the male (his payoff) are discounted by the probability that they do not reach adulthood; this in effect reduces the value of younger infants relative to older infants. While, in reality, S^j is probably somewhat lower than S^0 since the first, 'target' infant, infant 0, has already survived a certain amount of time, for the rest of this paper we assume that $S^j = S^0$. This assumption overestimates the probability of infanticide, but in species with many high-quality offspring, it will only produce a minor underestimation directly proportional to S^j/S^0 . In species with many low-quality offspring, the terms S^j and S^0 must be retained as the shape of the survivorship curve will have large effects on the outcome of the calculations. These inequalities also ignore any benefits other than increased paternity that may accrue to infanticidal males (e.g. reduced feeding competition for one's future offspring); such benefits could explain infanticide seen in seasonal breeders, although the model accurately predicts the reduced frequency of infanticide in populations with strongly seasonal breeding (van Schaik 2000b).

If males could identify their offspring, $P(p^0)$ would be 1 for the sire and 0 for every other male, possibly because of a change in paternal state (Elwood & Kennedy 1991). Thus, every nonfather

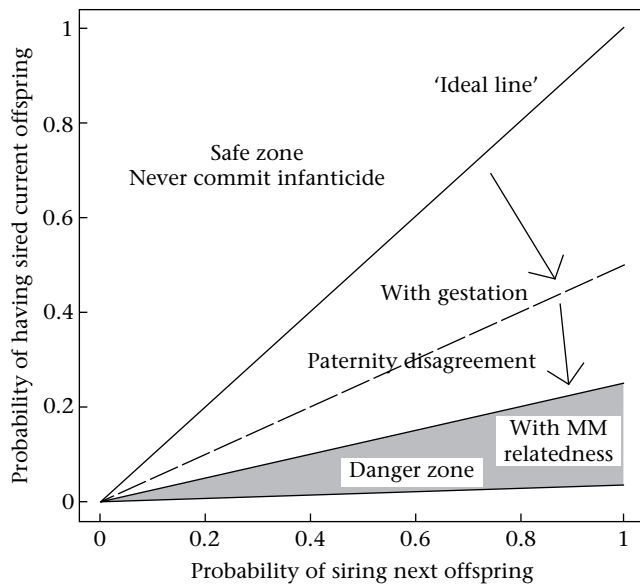


Figure 2. The conditions under which a male would increase his fitness by committing infanticide under the sexual selection hypothesis. The 'ideal line' represents the case where a male's estimated paternity in one infant (the 'current infant') is equal to his expected paternity in the next infant that a female would conceive if the male were to kill the current infant. Above this line, the male's probability of siring the female's next offspring, $E(p_i)$, is lower than the probability of his having sired her current infant, p^0 (upper left area). In this area, infanticide would never be adaptive. Below the ideal line, infanticide would be adaptive if the current infant and next infant required equal amounts of time until weaning. However, as the current infant usually cannot be killed by a male until after its birth, at minimum, it will be closer to weaning by at least the length of the species' gestation time. This reduces (by an amount equal to Gestation/IBI_{full}) the conditions under which infanticide is adaptive. Males should not commit infanticide unless they can gain a sufficiently larger share of paternity in the next (second) infant over the current (first) one to compensate for the time invested in the current offspring. The possibility of indirect fitness benefits through male–male relatedness would also serve to reduce the conditions under which infanticide is adaptive, such that males would only be infanticidal in the lower-right shaded area, the 'danger zone', described by inequality (3a). Increasing gestation:lactation ratios and male–male (MM) relatedness would decrease the incentive for infanticide and result in a larger 'paternity disagreement zone' in which males would accept, without committing infanticide, less paternity in the current offspring than they would expect to get in the next offspring. With a larger paternity disagreement zone, one would expect to find more male–male mating competition as a wider range of paternity probabilities would be accepted by all the males in a group before one became infanticidal.

male would become the equivalent of an extragroup male and would be expected to attempt infanticide under a very broad range of conditions, although this could be partially mitigated by indirect fitness and benefits tied to group size, such as cooperative vigilance. Still, in species where males cannot or do not effectively protect their offspring, it is likely to be in males' best interests, as well as in females' interests, for males not to be able to identify their own offspring. While not explicitly modelled here, an increased ability of males to recognize paternity would have the effect of reducing $P(p^0)$ for nonfather males and would therefore increase the infanticide risk to each infant. Unsurprisingly then, there is little evidence demonstrating male recognition of paternity from offspring phenotype at first contact with an infant (Elwood & Kennedy 1991; Paul et al. 1996; but see Buchan et al. 2003; Widdig 2007).

HOW SHOULD MALE MATING EFFORT RESPOND TO THE POSSIBILITY OF INFANTICIDE?

Researchers commonly view promiscuous mating as a female strategy to confuse paternity, thereby reducing the risk of

infanticide (e.g. Hrdy 1979). It is also generally assumed that males should always seek to maximize their paternity certainty. Little attention has been paid to the potential adaptive benefit that promiscuous mating may provide to males, despite the fact that half the genes in each infant protected by paternity confusion come from a male. While a number of researchers have noted that some male mammals choose to protect their offspring via their physical presence or territorial behaviours (even when this causes them to lose other mating opportunities, e.g. Harcourt & Stewart 2008), the fact that fathers may benefit from the protective effects of paternity confusion has thus far been neglected in the literature, especially in relation to its effects on males' mating effort and mate-guarding decisions. As infanticide is a threat in taxa lacking constant male vigilance against it (references in Agrell et al. 1998; van Schaik 2000b), males in these species may provide protection via paternity confusion.

Ignoring inclusive fitness for the moment, to maximize the benefit from a single offspring, a male must maximize the probability of his paternity in that offspring discounted by the probability that the offspring dies before reaching adulthood. Defining p^j as the focal male's paternity probability (the probability of having fathered infant j), we find the fitness value of the infant to the male, Val_j , by multiplying p^j by the probability that the infant is not killed, which is the joint probability that no male kills the infant and it does not die from extrinsic mortality, μ . This yields the following equation, given the terms defined in Table 2:

$$Val^j = p^j \times (1 - \mu) \times \prod_{k=1}^N \left(1 - \left[P(\text{Infanticidal}_k^j) \cap P(\text{Success}_k^j) \right] \right) \quad (5)$$

$P(\text{Infanticidal}_k^j)$ is essentially the probability that inequality (3a) will be true for another within-group male when the infant is born, although alternate infanticide models could be incorporated instead. In populations with male immigrants, $P(\text{Infanticidal}_k^j)$ would presumably be 1 for any immigrant. $P(\text{Success}_k^j)$ is a function of the number of males willing to defend the infant, the amount of time they spend in close proximity to the infant, the proportion of time that the infanticidal male is with the infant and the how successful defending males and females can be. As $P(\text{Infanticidal}_k^j)$ depends on p_k^j (the probability that male k fathered infant j) and paternity is a zero-sum game, p^j may be optimized at a value below 1. While it is possible that in some groups, males could be confused such that the sum of their perceived paternities is greater than 1, natural selection would probably select against this, possibly leading to a three-way evolutionary arm's race between the alpha male, the lower-ranking males and the female. This supposition could be tested with explicit game theoretic models.

Table 2
Definition of terms used in equations (5–8)

Term	Definition
Val^j	The benefit (in terms of genetic fitness) from infant j to the focal male
μ	The extrinsic infant mortality rate (cumulative from birth to reproductive independence)
p^j	The focal male's probability of being infant j 's father
N	The number of males in the group including those that immigrate into the group before the infant is weaned
$P(\text{Infanticidal}_k^j)$	The probability that male k would try to commit infanticide on infant j if given the opportunity
$P(\text{Success}_k^j)$	The probability that male k would succeed in an attempted infanticide of infant j
G	Gestation time

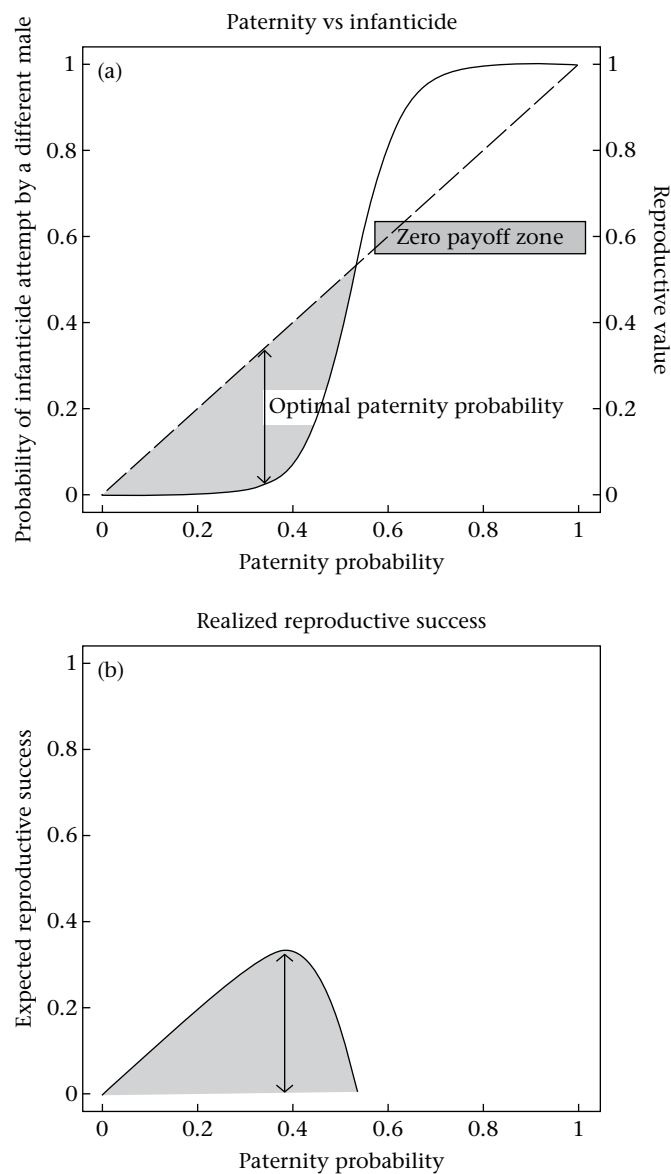


Figure 3. (a) A male's expected genetic representation in an offspring ('reproductive value') increases linearly with a male's paternity probability (p^j ; dashed line), but this increase can be negated by other males' infanticidal tendencies, which, aggregated, increase in a logistic fashion (solid line). The optimal paternity probability is the point that maximizes Val^j , the expected genetic representation in the infant, times the probability that the infant is not killed (represented by the arrow). The shaded area represents the area of positive net 'reproductive value', or the expected mean proportion of the male's genes in infants surviving to adulthood. (b) The relationship between reproductive success (Val^j), in terms of maximizing a male's genetic representation in offspring surviving to adulthood, and paternity probability (p^j) under the threat of infanticide without adequate protection. A male's reproductive success increases nearly linearly with increasing paternity probability at low paternity probability, but then sharply decreases as other males become infanticidal. As in (a), the shaded zone represents the area of positive net reproductive value and the arrow indicates the point at which the reproductive value is maximized.

The implications of equation (5) are presented in Fig. 3. The value at birth of each infant increases linearly with the paternity probability, while the probability that another male commits infanticide (assuming protector males cannot adequately defend the infant) increases dramatically once the threshold paternity probability for another male is crossed (Fig. 3a). Fig. 3b shows a male's expected reproductive success

(value of each surviving infant, based on the male's probability of paternity). Expected reproductive success increases linearly, then decreases sharply as other males become infanticidal.

Based on equation (5), it may seem that optimal paternity allocation should depend solely on the ability of other males to commit infanticide and on the expected paternity probability of each male in subsequent matings. As the ability of males to commit infanticide and the expected paternity probability of males in each state would be species-specific quantities that natural selection could act upon, one might predict that there should be little disagreement in terms of paternity allocation among the males and between the males and female, as both mothers and potential fathers lose out when infanticide is committed, so all have an interest in a relatively equitable distribution of paternity. Equation (5) does generally predict somewhat reduced paternity allocation disagreement among individuals, compared to current theory, which holds that each male is trying to maximize only his probability of paternity. However, examining Fig. 2 and inequalities (1a)–(3a), one can discern that the gestation time and any male–male relatedness increase the ability of males to compete over some 'extra' paternity probability as males have some flexibility in increasing their paternity at the expense of others because of indirect fitness and the 'sunk time' represented by gestation. Thus, mating competition should not be reduced to zero.

Under this model, a male could safely increase his paternity probability when male–male relatedness increases, infant defensibility increases, when the lactation period is extended relative to the gestation period or when male dominance hierarchies become more stable. Inclusive fitness could be modelled as an additive factor to p^j as was done in inequalities (1a)–(3a). Such an addition would cause a male's Val^j to start at a higher value than 0 when $p^j = 0$ and then increase somewhat more slowly with increasing p^j . This would not qualitatively change any of the aspects of the model, however.

Hypothetical examples illustrate the general principles that emerge from this model, which assumes the absence of effective protection of infants. Species with fission–fusion social organization, those that 'park' or leave their infants to forage and those in which females forage alone with their offspring should particularly adhere to the assumption that males are unable to protect infants, although other species may also do so. In the first example, we assume a group consisting of two unrelated males (α and β) with no immigration. To operationalize equation (5), we assume that there is no extrinsic mortality, use a gestation:interbirth interval ratio (G/IBI_{full}) of 0.3 ($IBI_{full} - G$ is the maximum possible IBIReduction) and assume a probability of rank change of 0.2, such that $P(\beta|\alpha) = P(\alpha|\beta) = 0.2$ and $P(\alpha|\alpha) = P(\beta|\beta) = 0.8$. We further assume that the only condition relevant to state (and therefore to expected paternity probability of future offspring) is rank. Equation (5) requires that we assign state-specific paternity probabilities a priori. While this runs the risk of being characterized as circular reasoning, it does accurately represent the fact that, on average, natural selection should favour decisions based on the expected paternity for males at a given rank. This can be thought of as the result of an iterative process that reflects a male's ability to monopolize oestrous females and defend infants from other males. In this case, we use $E(p_\alpha) = 0.7$ and $E(p_\beta) = 0.3$ for the paternity expectations of the α male and β male, respectively. We model the $P(\text{Infanticidal}_k^j)$ as a step function using the decision rule from inequality (3). So, equation (5) for the α and β males, respectively, becomes:

$$\alpha : \text{Max}(\text{Val}^j) = \text{Max} \left[P_\alpha \times P(\alpha|\beta) \left(1 - \left(\begin{array}{l} 1 \text{ if } E(\alpha) \left(1 - \frac{G}{\text{IBI}} > p(\beta) \end{array} \right) \right) \right) \times P(\beta|\beta) \left(1 - \left(\begin{array}{l} 1 \text{ if } E(\beta) \left(1 - \frac{G}{\text{IBI}} > p(\beta) \end{array} \right) \right) \right) \right] \quad (6a)$$

$$\beta : \text{Max}(\text{Val}^j) = \text{Max} \left[p_\beta \times P(\beta|\alpha) \left(1 - \left(\begin{array}{l} 1 \text{ if } E(\beta) \left(1 - \frac{G}{\text{IBI}} > p(\alpha) \end{array} \right) \right) \right) \times P(\alpha|\alpha) \left(1 - \left(\begin{array}{l} 1 \text{ if } E(\alpha) \left(1 - \frac{G}{\text{IBI}} > p(\alpha) \end{array} \right) \right) \right) \right] \quad (6b)$$

Similar reasoning can also give a fitness-maximizing equation for the female, although in a complete model the possible genetic costs of mating with an inferior male should be taken into account, as in equation (7):

$$F : \text{Max}(\text{Val}^j) = (1 - P(\text{SuboptimalPaternity})\text{Cost}(\text{SuboptimalPaternity})) \times (1 - \mu) \times \prod_{k=1}^N P(\text{Infanticidal}^j_k) \cap P(\text{Success}^j_k) \quad (7)$$

Assuming the cost of mating with genetically inferior males is negligible compared to the cost of infanticide, equation (7) becomes:

These calculations show that the female's optimal paternity probability allocation matches much more closely the paternity probability allocation favoured by the male most likely to be β male when the infant is born. This is a general feature of this model; higher-ranking males can sometimes afford to accept a certain probability of infanticide if lower-ranking males overtake them in rank, while lower-ranking males must allow higher-ranking males enough paternity to definitely prevent them from committing infanticide. The model also implies that committing infanticide against one's own offspring could be favoured; about 4% of the time, the β male would be expected to take over the α position and kill his own offspring (assuming males cannot reliably identify their

$$F : \text{Max}(\text{Val}^j) = 1 \times P(\alpha|\beta) \left(1 - \left(\begin{array}{l} 1 \text{ if } E(\alpha) \left(1 - \frac{G}{\text{IBI}} > p(\beta) \end{array} \right) \right) \right) \times P(\beta|\beta) \left(1 - \left(\begin{array}{l} 1 \text{ if } E(\beta) \left(1 - \frac{G}{\text{IBI}} > p(\beta) \end{array} \right) \right) \right) \times P(\beta|\alpha) \left(1 - \left(\begin{array}{l} 1 \text{ if } E(\beta) \left(1 - \frac{G}{\text{IBI}} > p(\alpha) \end{array} \right) \right) \right) \times P(\alpha|\alpha) \left(1 - \left(\begin{array}{l} 1 \text{ if } E(\alpha) \left(1 - \frac{G}{\text{IBI}} > p(\alpha) \end{array} \right) \right) \right) \quad (8)$$

The results of solving this system of equations are given in the first row of Table 3. The α male should attempt to gain 79% paternity probability, accepting that the β male will commit infanticide 20% of the time when he rises in rank to α , yielding an overall Val^j_α (the α males' reproductive success due to infant j) of 0.632. The β male's optimal paternity probability is 51%; at this level, the infant is not at risk from infanticide. The female prefers any α male paternity probability between 0.49 and 0.51, as these values define the region in which neither male would ever want to commit infanticide. The second row of Table 3 shows the results of the same system of equations taking the probability of a rank change as 0.8, as when a rank reversal was imminent when conception occurred. The values for the two males are reversed from the values above, while the female's optimal paternity remains unchanged (although this need not always be the case).

offspring phenotypically). While there is disagreement between the males over optimal paternity allocation (varying from 0.79 to 0.49 for the α male, according to the wishes of the α male and β male, respectively), both males should allow the other male a certain proportion of matings. In some animals, such as Belding's ground squirrels, *Spermophilus beldingi*, multiple paternity within litters serve as direct evidence of the efficacy of paternity distribution (Hanken & Sherman 1981). Field vole females, *Microtus agrestis*, mate promiscuously in the laboratory only when males are close together, but when the males are further apart, females only mate with the dominant male (Agrell et al. 1998). This would suggest that, in this species at least, males acquiesce to some female promiscuity when it may be difficult to prevent infanticide.

According to this model, the key factor in determining optimal paternity allocation is a male's expected rank when the infant is

Table 3

The optimal allocation of paternity for each individual in a group with two males

Rank change probability	α : optimal p_α	α : optimal Val^j	$P(\text{infanticide})$ at α optimum	β : optimal p_β	β : optimal Val^j	$P(\text{infanticide})$ at β optimum	F: optimal $p(\alpha)$	$P(\text{infanticide})$ at F optimum
0.2	0.79	0.632	0.2	0.51	0.51	0	0.49–0.51	0
0.8	0.51	0.51	0	0.79	0.632	0.2	0.49–0.51	0
0.02	0.79	0.774	0.02	0.51	0.51	0	0.49–0.051	0

The optimal allocation of paternity for each individual in a group with two males along with the 'value' (Val^j) of the infant to the individual and the probability of infanticide at that optimum. Note that for each column, the value is the optimal value for the individual referred to before the colon. F = female; α = α male; β = β male. Row 1 depicts a situation where there is a relatively low (0.2) probability that the two males will reverse ranks between the time of conception and birth, while row 2 represents a situation where there is a relatively high (0.8) probability of a rank reversal during that time. Row 3 depicts a very stable hierarchy; in this example the desired paternity allocation does not change, although the probability of infanticide decreases. Parameters: $p(\alpha)$ is the probability that the α male is the offspring's sire, while $p(\beta)$ is the probability that the β male is the offspring's sire, $P(\text{infanticide})$ is the probability that the offspring is killed by an infanticidal male, and Val^j refers to the value, in terms of reproductive success, of the infant to the potentially infanticidal male, and is the joint probability that the male is the infant's father and that it survives to adulthood. Note that the female's optimal allocation matches the β male's optimal allocation more closely. See text for the full model parameterization used.

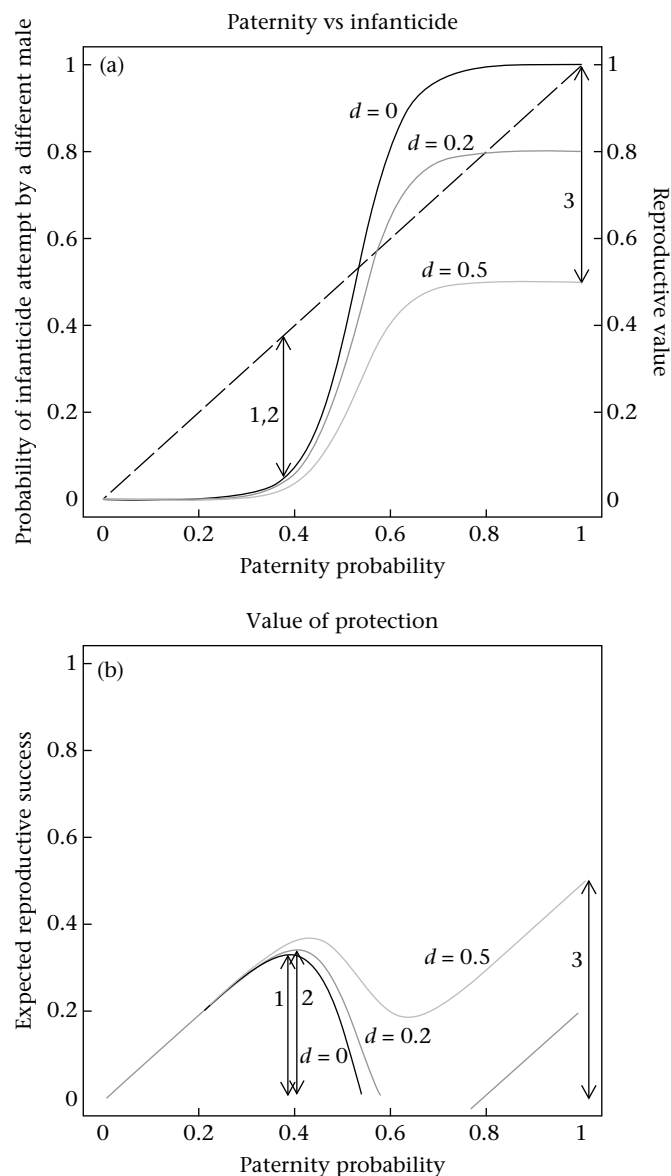


Figure 4. (a) A male's expected mean genetic representation in an offspring increases linearly with a male's paternity probability (p_i^j ; solid straight line) while infanticide probability increases as a logistic function (as in Fig. 3a). However, this increase can be tempered by protection of infants. The logistic lines indicate different values for the 'defence factor', d , (reduction in $P(\text{Success}_k)$), or the probability that an infant is ever killed by an infanticidal male: solid line = 0, dashed line = 0.2, dashed and dotted line = 0.5. The arrow labelled 1, 2 is placed approximately at the global optimum paternity probability for males with defence factors of 0 and 0.2 (just below $p = 0.4$; in reality, the precise optimum differs slightly between these two defence factors) and the arrow labelled 3 is placed at the global optimum paternity probability for males with a defence factor of 0.5 (at $p = 1.0$). (b) The relationship between expected reproductive success (Val^j) and paternity probability, p_i^j , under the threat of infanticide with various levels of protection. The fitness curves have two local optima, one at $p = 1$ and the other between 0.35 and 0.45. Which of the two is the global optimum depends on parameter values; the vertical lines are drawn at the global optimum for each parameterization (1 at $d = 0$, 2 at $d = 0.2$, 3 at $d = 0.5$). Note that the defence factor can include both male and female defence of the infant.

born, not when it is conceived. Thus, this model makes an opposite prediction from life-history trade-off theory; at the end of a male's reign as α male, he should voluntarily allow rising males to take some of 'his' paternity.

The third row of Table 3 describes a situation where there is a very stable hierarchy; the probability of rank change is only 0.02,

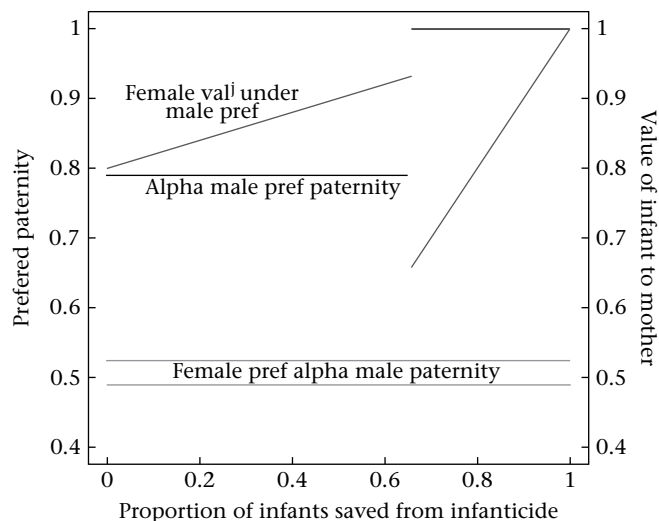


Figure 5. Increasing infant protection (i.e. increasing defence factor, d) shifts the α male's preference to the higher fitness peak at $p_\alpha = 1$ (dashed and dotted line). Above a certain threshold (jump discontinuity), the male attempts to ensure paternity and monopolize matings, which leads to a reduction in the female's chances of producing a surviving offspring at intermediate to high protection values (dashed line). For a wide array of values of parameters, females prefer polyandry at all protection values less than 1 (female preference is the area between the two solid lines). Female's Val^j is defined as in equation (8) as the probability that a female's infant j survives to adulthood; it ignores 'good genes' effects where one possible sire produces better children, on average, than another possible sire.

while the other variables remain the same as in the above described examples. In this case, the optimal paternity allocation does not change from the moderately stable hierarchy described above, but the probability of infanticide decreases. In general, more stable hierarchies promote decreased incidence of infanticide since it is relatively unlikely that a male will have a higher expectation of paternity for a female's next offspring than he has for her current one.

Optimal Mating Effort with Infant Defence

To demonstrate the effect of infant defence on optimal paternity allocation, we will first examine a simplistic model including infant defence. This model assumes the same parameters as the above model, but includes a 'defence factor', d , that reduces by a constant proportion the probability of an infant ever being killed, which can be modelled by decreasing $P(\text{Success}_k)$ in equation (5) from 1 to $1 - d$. The qualitative result is displayed in Fig. 4, which shows the impact of infant defence of varying degrees of success on the expected reproductive success of males, based on their paternity probability.

Imperfect infant defence creates a fitness landscape with two local optima. Which optimum is higher varies depending on parameters. One local optimum corresponds to the previously discussed optimal paternity, which prevents at least some other males from becoming infanticidal. A second local optimum exists at $p_i = 1$. Male mammals face a choice between two distinct strategies: a male can either choose to protect his young and attempt to gain 100% paternity probability of those young, or choose to forgo protecting his young and allow other males to gain enough paternity that his direct protection is not required. This decision may be a species-level evolved strategy, a within- or between-population polymorphism, or a choice or series of choices at the individual level. Of course both strategies can fail; protectors can weaken, die or simply fail, and new or low-ranking males can rapidly rise in rank and become

infanticidal even when males attempt to distribute paternity. However, these results suggest a clear dichotomy in strategies; males should not attempt levels of paternity intermediate between the two local optima. Elements of a species' or population's socioecology should determine which strategy males will follow. Explicitly incorporating inclusive fitness into this model would have the effect of increasing the male's Val^I at the lower optimum relative to the higher one since at $p_i = 1$, there can be no inclusive fitness benefit.

Figure 5 depicts how infant protection modifies the disagreement over paternity allocation between the α male and the female. Somewhat unintuitively, an increase in a male's ability to protect an offspring should increase the disagreement over optimal paternity allocation between the α male and female, unless that protection is ineffective or extremely effective. At intermediate levels of protection, the male's Val^I_α increases quickly with increasing p_α , while there is not a concomitant rise in the female's Val^I . At perfect protection, the female should be indifferent between monopolization by one male and polyandry (setting aside potential 'good genes' arguments, e.g. benefits from mating with a successful protector male or the benefits of inducing sperm competition). This qualitative result can be generalized to a wide variety of realistic parameter values and group sizes. However, in some large group sizes, it may be impossible to totally mitigate the possibility of infanticide since paternity cannot be distributed evenly enough for all males to be noninfanticidal if they became α ; in these cases the female's interests may somewhat more closely align with the α male's paternity allocation. For example, in a situation where there are five unrelated males with $E(p_\alpha) = 0.45$, $E(p_\beta) = P(\alpha|\beta) = 0.25$, $E(p_\gamma) = P(\alpha|\gamma) = 0.15$, $E(p_\delta) = P(\alpha|\delta) = 0.1$, $E(p_\epsilon) = P(\alpha|\epsilon) = 0.05$ and all other parameter values the same as the model from equations (6)–(8), the female is content as long as she suffers no risk of infanticide from the α or β male and does not suffer infanticide risk from the other males as long as they do not rise to α .

This result could help explain the evolution of female hypersexuality and increased ovulation confusion in bonobos, *Pan paniscus* (Wrangham & Peterson 1996; Reichert et al. 2002). The following is one possible scenario. Female bonobos with an increased ability to form groups (relative to chimpanzees) would have led to an increased, but most likely not perfect, ability of male bonobos to protect infants from other males. Bonobos may have fallen in the portion of Fig. 5 where increased male protection of infants led to reduced female reproductive success but increased the reproductive success of α males. This would have increased the incentive for those males to attempt to monopolize females, and could have prompted females to adopt counterstrategies, of which more concealed ovulation and longer sexual attractiveness may have been relatively easy to adopt, since they are exaggerations of mechanisms that were presumably already present in the common ancestor of chimpanzees and bonobos. With sufficiently reduced ability to determine paternity, males would lose the incentive to protect infants or to attempt to monopolize females. Even in chimpanzees, high-ranking males allow females outside of maximal tumescence to mate with other males, consistent with the predictions of this model (Deschner et al. 2004; Stumpf & Boesch 2005). This model, in fact, accords well with the graded signal hypothesis (Nunn 1999), but implies that graded fertility signals may in fact incidentally benefit all parties, not just females. Reliable indicators of the probability of conception could mitigate competition through temporal spacing of matings with high and low probability of conception. With conspicuous female signals, high-ranking males can allow lower-ranking males to achieve matings that are relatively unlikely to result in offspring, while lower-ranking males can defer to higher-ranking males (or attempt only sneak copulations) when conception is likely.

DISCUSSION

At this point, it is useful to review the conditions favouring a rise in mating competition, and presumably therefore reproductive skew, under the assumptions of the model we present here. While a complete set of equations that accurately encapsulated all relevant variation would be cumbersome, some factors are predicted to be particularly important. In particular, a higher gestation:lactation ratio, decreased male:female ratio, higher male–male relatedness (male philopatry), breeding seasonality (although its effects on the operational sex ratio would somewhat mitigate its influence), increased infant defensibility by males or females (greater female–female cohesion and male day range:female day range ratio, lower sexual dimorphism), longer α male tenure and increased male rank stability would be predicted to increase the possible mating competition within a group or population. All these changes would allow high-ranking males to increase their paternity probability without concomitant increases in infanticide risk, and would presumably result in increased reproductive skew, or the tendency for paternity to be concentrated among the highest-ranking males. Even under such conditions, females may still attempt to distribute paternity more evenly to buffer themselves against the dangers of potential rank reversals.

While this model predicts that extragroup males should be the most likely perpetrators of infanticide, it also predicts that, under some conditions, within-group infanticide should occur, particularly by newly (and soon-to-be) high-ranking males in populations with high reproductive skew. This prediction is supported by observations of some wild populations (examples cited in van Schaik 2000b). Our model implies that, in contrast to most previous assumptions, not all within-group infanticide is maladaptive and pathological, and that the circumstances surrounding each observed case of infanticide should be carefully considered with respect to the infanticidal male's reproductive success. Doing so may help explain currently puzzling instances of infanticide, including those committed by potential, or actual, fathers (e.g. Kawanaka 1981; Crockett & Sekulic 1984; Hasegawa 1989; Feh & Munkhtuya 2008). This model also cautions against ascribing infanticide to new immigrants by default, as is frequently done (van Schaik 2000b). While new immigrants are the most likely to commit infanticide, within-group males should not necessarily be ruled out in the absence of direct evidence.

This model also predicts that a male at the waning end of his tenure should permit other males a fairly high paternity probability for each new infant conceived. This is contrary to the prediction of basic life history theory, which would hold that organisms that are not likely to have much chance for reproduction in the future should put all their effort into reproduction in the present (Roff 1992). In general, α males and resident males should allow other males to mate with females, within limits, when they cannot very effectively defend infants from infanticide. Observations in Japanese macaques, *Macaca fuscata*, may reflect a case of this; nonresident males obtain a significant, but less than expected given random mating, proportion of matings in a number of study populations and are also somewhat likely to rise to high rank quickly if they do immigrate (Sprague 1992). This may suggest that resident males or females (or both) are conceding just enough paternity to reduce the potential threat of infanticide. Alternatively, males may simply be unable to prevent those matings.

Females and lower-ranking or nonresident males should generally agree more on the optimal paternity probability distribution than females and α males or resident males, suggesting that β males should spend most of their reproductive effort on male–male competition, while α males may need to expend more effort in female coercion. The model also predicts that the infanticide

defence success rate required by females to accept monopolization by one male should be higher than that required by males to attempt monopolization of a female. With the exception of species in which males can offer perfect protection of infants, females should seek extrapair sneak copulations with males other than the one attempting to monopolize them. This model also suggests that species less able to defend their infants should be patrilocal to reduce infanticide pressure by increasing male–male relatedness. It further predicts infanticide risk from possible sires should be highly concentrated at the youngest infant ages when it is most likely to be adaptive for a male that may be related to the target infant. Finally, the model suggests that, as the number of potential sires in a group increases, the age at which an infant's risk from unrelated extra-group males should decrease.

While we have applied the model above to males' decisions about a single infant or female, the same framework can be used to examine the broader evolutionary decisions of males in populations. This model suggests that there are two distinct strategies that male mammals can use: they can either defend offspring and try to maximize their chances of paternity at each conception, or not defend offspring but allow other males some chance of paternity. This does not imply that those males that do not monopolize females would not defend infants when it paid them to do so, but it does suggest a dichotomy of fundamental strategies. Which of these two fundamental strategies mammalian males adopt can undoubtedly be tied to basic socioecological parameters. Using the framework presented above, one could solve the optimization over the life span of a male adopting different mating and parenting strategies to determine which strategy accrues the highest long-term payoffs, summed over all potential infants he could sire. Explicit game theoretic models incorporating immediate trade-offs to increased mate guarding into the above model would add a further, probably important, element of complexity. Optimal skew and incomplete control models of (generally female) group reproductive output control from behavioural ecology also provide a template for some potentially useful additional avenues of theoretical enquiry. Indeed, incomplete control models, in which dominant animals must exert effort to attempt to increase their share of the group's total reproduction, seem to share particularly promising logical parallels to this situation (Reeve et al. 1998). Such analyses might help explain observed diversity in mammalian social systems, and could identify species that do not conform to expectations as potential foci for future research.

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