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Reproductive skew and indiscriminate infanticide

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In communally breeding animals, there is an evolutionary conflict over the partitioning of reproduction within the group. If dominant group members do not have complete control over subordinate reproduction, this conflict may favour the evolution of infanticidal behaviour (by either subordinates or dominants or both). Elimination of offspring, however, is likely to be constrained by the difficulty of discriminating between an individual's own progeny and those of cobreeders. Here, we develop an evolutionarily stable strategy (ESS) model of reproductive partitioning, which demonstrates that killing of young can be favoured, even if such discrimination is not possible. The model predicts that infanticide will typically be associated with elevated levels of offspring production, and is most likely to prove evolutionarily stable when the coefficient of relatedness between cobreeders is low, and offspring are cheap to produce. The effect of infanticide is to release subordinates from the reproductive restraint they would otherwise be forced to exercise, leading to reduced reproductive skew. When infanticide is possible, addition of numerous young to the joint brood will not lower overall productivity, because progeny in excess of the most productive brood size are eliminated. Subordinates are thus free to contribute more young to the brood than would otherwise be the case. In addition, we show that the possibility of infanticide may influence the pattern of reproduction within a group even if no offspring are actually killed at equilibrium.

Animal societies vary widely in the distribution of reproduction among individuals (Keller & Reeve 1994). At one extreme are those that exhibit a high level of reproductive skew, with one or a few individuals monopolizing direct reproduction; examples include the colonies of many eusocial ants (Hölldobler & Wilson 1990; Bourke & Franks 1995), and of the naked mole-rat, *Heterocephalus glaber* (Jarvis 1991). At the other extreme are low-skew societies, for example, the multiple-queen colonies of some polistine and polybiine wasps (see Bourke 1997), or vertebrate societies such as those of the banded mongoose, *Mungos mungo* (Rood 1986) or groove-billed ani, *Crotophaga sulcirostris* (Vehrencamp et al. 1988), in which reproduction is shared equally between group members.

What determines the stable level of skew in any particular society? Until recently, models of reproductive partitioning have made the simplifying assumption that reproductive competition will always be resolved in favour of the dominant members of the group, who can exert full control over the allocation of breeding opportunities (Vehrencamp 1979, 1983a, b; Reeve & Ratnieks 1993; Reeve & Keller 1995; Johnstone et al., in press). Subordinates are thus expected to receive a share of direct reproduction only if this incentive is needed to persuade them to stay and help with offspring care, rather than leaving or fighting to achieve dominance themselves. In reality, however, control of breeding by dominants may often be incomplete or absent, so that subordinates can claim a degree of unsanctioned reproduction for themselves (Reeve & Ratnieks 1993; Cant 1998; Clutton-Brock 1998; Reeve et al. 1998).

When dominants cannot entirely prevent subordinates from breeding, they stand to gain by eliminating unsanctioned young; equally, subordinates stand to gain by eliminating (if they can) the rival young of dominants. Incomplete control of reproduction in communal breeders thus sets the stage for the evolution of infanticide (e.g. Mumme et al. 1983; Koford et al. 1990; Bourke 1991; Heinze et al. 1992; Medeiros et al. 1992; Reeve & Nonacs 1992; Koenig et al. 1995). Infanticidal behaviour may, in turn, affect the payoffs that dominants and subordinates stand to gain by producing young, and thus influence the pattern of reproduction within the group.

While the benefits of eliminating the offspring of competitors are clear, infanticidal behaviour is often likely to be constrained by the difficulty of distinguishing

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between an individual's own progeny and those of other group members (Polis 1984; Reeve & Ratnieks 1993). In communal breeders, the spatial and temporal clues to offspring identity that might be employed under other circumstances are of little use, making the problem of identification especially difficult. Nevertheless, despite the costs that may be incurred through incidental destruction of an individual's own progeny, there seem to be circumstances under which indiscriminate infanticide can be evolutionarily stable. Bourke (1991, 1994), for instance, demonstrated experimentally that queen ants of the species *Leptothorax acervorum*, which engage in high rates of egg cannibalism within their polygynous societies, do not discriminate between their own and a nestmate's eggs.

Here, building on the framework of Cant (1998), we develop a simple evolutionarily stable strategy (ESS) model of reproductive partitioning that incorporates the possibility of indiscriminate infanticide. We determine the circumstances under which infanticide is most likely to prove stable, and investigate its effects on the pattern of reproduction within the group. We show that although indiscriminate destruction of offspring cannot directly alter the level of reproductive skew (see Bourke 1994), it may do so indirectly through its effects on the reproductive behaviour of dominants and subordinates.

THE MODEL

We focus on the division of reproduction between two cooperatively breeding individuals, referred to as Alpha and Beta. The coefficient of relatedness between the two is denoted r. Each must decide on the number of offspring that she will produce (denoted n in the case of Alpha, and m in the case of Beta), and is assumed to choose the number that maximizes her own inclusive fitness. As in previous analyses of reproductive skew (e.g. Vehrencamp 1983a, b; Reeve & Ratnieks 1993), we model the situation as a sequential game (see Maynard Smith 1982; Reeve 1998), in which Beta's decision is conditional on Alpha's. We do not consider the issue of subordinate departure, instead assuming that the survival prospects for a lone individual who disperses away from the association are sufficiently poor always to favour remaining (nor do we address the possibility of uncertain arrival of a subordinate).

Offspring fitness (which is the same for all the members of the brood) is a decreasing function of total brood size t ($=n+m$). For simplicity, we assume that the probability of an individual offspring surviving to maturity, denoted $s(t)$, is given by

$$s(t)=1-kt \tag{1}$$

that is, offspring fitness declines linearly with t, at a rate determined by k (other decreasing functions yield qualitatively similar results). The fitness cost of producing young (which is the same for both Alpha and Beta) is directly proportional to the number produced; the constant of proportionality is denoted μ.

The situation described above corresponds to the 'extended model' of Cant (1998), who showed that the evolutionarily stable numbers of young produced by Alpha and by Beta, denoted n^* and m^*, respectively, are as follows:

$$\text{For } r<\sqrt{2}-1,\ n^*=\frac{1-\mu}{k(2-r(1+r))}$$

$$\text{and } m^*=\frac{1-\mu}{2k}-\frac{(1+r)n^*}{2} \tag{2a}$$

$$\text{For } r\geq\sqrt{2}-1,\ n^*=\frac{1-\mu}{k(1+r)} \text{ and } m^*=0 \tag{2b}$$

These equations imply that, above a critical level of relatedness, the dominant produces sufficient offspring to ensure that the subordinate does best to refrain from reproducing at all (the lower the relatedness between the two, the more offspring the dominant must produce to ensure that this is the case). Below this critical level, it pays the dominant to reduce its production, allowing the subordinate to contribute some young to the joint brood (this corresponds to Reeve & Keller's (1997) suggestion that a dominant may benefit by yielding a share of reproduction to the subordinate, in order to prevent her acting selfishly, in this case by adding young to the brood in excess of the most productive size).

Let us now suppose that after production of offspring, either Alpha, Beta or both can commit infanticide. To be more precise, we assume that either breeder can kill or eject from the brood any number i ($\leq t$) of young, at no cost to herself, but that she cannot distinguish between her own progeny and those of her cobreeder. Thus any offspring that are killed are chosen effectively at random. Under what circumstances does it pay to eliminate some of the brood, and how does the possibility of infanticide influence the values of m^* and n^*?

When Does Brood Reduction Pay?

Since neither breeder can identify her own young, it pays both Alpha and Beta to commit infanticide only if, by doing so, they can increase the total number of offspring that survive to maturity from the joint brood. From equation (1), we know that the number of offspring surviving from a brood of size t is equal to

$$t(1-kt)$$

and that the most productive brood size (which yields the most surviving offspring), denoted $\hat{t}$, is therefore given by

$$\hat{t}=\frac{1}{2k}$$

The optimal choice of action is thus to refrain from infanticide whenever total brood size t($=m+n$) is less than $\hat{t}$, and otherwise to eliminate just enough offspring to reduce t to $\hat{t}$ (note that there is no conflict between the two breeders over the optimum level of infanticide).

The above implies that if the solution specified by equation (2) yields a total brood size less than $\hat{t}$, then the possibility of infanticide has no effect on the outcome of the model (because the stable brood size in equation (2) is small enough to render it unprofitable). Only if equation (2) specifies a total brood size greater than $\hat{t}$ do we need to take infanticide into account, and recalculate the stable levels of offspring production n^* and m^*.

Infanticidal Equilibria

Assuming that the possibility of infanticide is relevant, let us first consider the possibility of an equilibrium at which Alpha and Beta jointly produce a brood larger than $\hat{t}$ and infanticide actually takes place. At such an equilibrium, the inclusive fitness payoffs to each individual from reproduction, denoted w_α for Alpha and w_β for Beta, are given by

$$w_\alpha = \frac{n+rm}{n+m}\hat{t}(1-k\hat{t}) - \mu(n+rm) \tag{3a}$$

$$w_\beta = \frac{rn+m}{n+m}\hat{t}(1-k\hat{t}) - \mu(rn+m) \tag{3b}$$

These formulae assume that total brood size after infanticide has taken place is always equal to $\hat{t}$, regardless of the values of n and m, since enough offspring will always be eliminated to reduce it to this level. In each case, the inclusive fitness payoff is equal to the mean relatedness of offspring to the parent in question, multiplied by total brood size after infanticide ($\hat{t}$) and by offspring survival, minus the costs of offspring production to the parent itself and to its cobreeder (the latter being devalued according to the coefficient of relatedness between the two).

To obtain Beta's optimum number of offspring given that Alpha has produced n young of her own, which we denote $\hat{m}(n)$, we differentiate equation (3b) with respect to m, and solve for $dw_\beta/dm=0$. This yields the following unique positive solution

$$\hat{m}(n) = \sqrt{\frac{(1-r)\hat{t}(1-k\hat{t})n}{\mu}} - n = \sqrt{\frac{(1-r)n}{4k\mu}} - n \tag{4}$$

(it can easily be shown that $\hat{m}(n)$ represents a fitness maximum rather than a minimum). If we now replace m in equation (3a) with $\hat{m}(n)$, we obtain Alpha's inclusive fitness payoff assuming that Beta will respond optimally to her choice of brood size, which we denote $\hat{w}_\alpha$

$$\begin{aligned}\hat{w}_\alpha &= \frac{n+r\hat{m}(n)}{n+\hat{m}(n)}\hat{t}(1-k\hat{t}) - \mu(n+r\hat{m}(n)) \\ &= \frac{n+r\left(\sqrt{\frac{(1-r)n}{4k\mu}}-n\right)}{n+\left(\sqrt{\frac{(1-r)n}{4k\mu}}-n\right)}\hat{t}(1-k\hat{t}) \\ &\quad - \mu\left(n+r\left(\sqrt{\frac{(1-r)n}{4k\mu}}-n\right)\right)\end{aligned} \tag{5}$$

Finally, to obtain Alpha's optimum number of young, n^*, taking into account the influence of her choice on Beta's subsequent decision, we differentiate equation (5) with respect to n, and solve for $d\hat{w}_\alpha/dn=0$. This yields the following unique solution

$$n^* = \frac{(1-r)\hat{t}(1-k\hat{t})}{4\mu} = \frac{(1-r)}{16k\mu} \tag{6}$$

which represents Alpha's evolutionarily stable level of offspring production (it can easily be shown that n^* represents a fitness maximum rather than a minimum). The corresponding value for Beta, m^* $(=\hat{m}(n^*))$, is then given by equation (4)

$$m^* = \hat{m}(n^*) = \sqrt{\frac{(1-r)n^*}{4k\mu}} - n^* \tag{7}$$

Substituting into the above the expression for n^* given in equation (6), we obtain, after some rearrangement, the following simple result

$$m^* = \frac{(1-r)}{16k\mu} = n^* \tag{8}$$

In other words, at an infanticidal equilibrium, both Alpha and Beta produce the same number of offspring, which decreases with increasing relatedness, cost of offspring production and degree of density dependence in offspring survival.

The evolutionarily stable number of young that are killed, i^* $(=n^*+m^*-\hat{t})$, is given by

$$i^* = \frac{(1-r)-4\mu}{8k\mu} \tag{9}$$

which implies that the proportion of the total brood succumbing to infanticide, $i^*/(n^*+m^*)$, is given by

$$\frac{i^*}{n^*+m^*} = 1 - \frac{4\mu}{1-r} \tag{10}$$

In other words, the proportion of young killed decreases with relatedness and with the cost of production. Since elimination of a negative number of offspring is impossible, however, the solution specified by equations (6), (8) and (9) is valid only for

$$i^*>0 \Leftrightarrow r<1-4\mu \tag{11}$$

Noninfanticidal Equilibria

If condition (11) is not met, no infanticidal equilibrium exists. Instead, Alpha's inclusive fitness decreases with the number of offspring produced for all values large enough to favour infanticide. At the same time, since equation (2) yields a solution for which $t>\hat{t}$, we may conclude that Alpha's inclusive fitness increases with the number of offspring produced for all values small enough to render infanticide unprofitable. Under these circumstances, Alpha does best to produce just enough offspring to ensure that total brood size (taking into account the influence of her choice on Beta's reproductive decision) equals $\hat{t}$. n^* therefore satisfies

$$n^* + \hat{m}(n^*) = \hat{t}$$

which, with equation (4), yields (after some rearrangement)

$$n^* = \frac{4k\mu\hat{t}^2}{1-r} = \frac{\mu}{k(1-r)} \qquad (12)$$

The equilibrium number of offspring produced by Beta, m^* ($=\hat{m}(n^*)$), can then be calculated by substituting equation (12) into equation (4), and is given by

$$m^* = \frac{(1-r)-2\mu}{2k(1-r)} \qquad (13)$$

Although the stable solution specified by equations (12) and (13) does not feature infanticide (since total brood size does not exceed $\hat{t}$), it still differs from the original values of n^* and m^* given in equation (2). In other words, by incorporating the possibility of infanticide into the model we have changed the evolutionarily stable outcome, even though no young are actually killed at equilibrium.

The equilibrium number of offspring for Alpha specified in equation (12) increases with μ, the cost of production (by contrast with equations (2) and (6), which imply that fewer offspring will be produced when μ is greater). The reason is that when costs of production are higher, Beta will tend to contribute fewer young to the brood, so that Alpha can afford to produce more offspring without triggering infanticide.

RESULTS

In this section, we first present an illustrative sample of solutions to the model, and then summarize graphically the effects of the three parameters k (the rate at which offspring survival declines with increasing brood size), r (relatedness) and μ (the cost of producing offspring), on the evolutionarily stable outcome (focusing on the level of infanticide, total brood size and degree of reproductive skew at equilibrium).

Figure 1 shows the stable numbers of young produced by Alpha and Beta, together with total brood size (prior to any infanticide) and the number of offspring eliminated, as a function of relatedness between the two breeders. For sufficiently high levels of relatedness (here r>0.6), the incorporation of infanticide in the model has no effect, and our results match those of Cant (1998). In the case illustrated in the figure, Beta refrains from reproduction, while Alpha produces an increasing number of offspring as r decreases. Below a critical point (here r=0.6), however, the possibility of infanticide begins to have an effect, acting to stabilize total brood size at the most productive level (by reducing the benefits that Alpha stands to gain from production of additional young). Alpha now produces fewer young as r decreases, while Beta adds an increasing number of offspring to the joint brood. Finally, below a second threshold level of relatedness (here r<0.2), infanticide is actually stable. Both Alpha and Beta produce the same number of young, which increases as r falls, and offspring in excess of the most productive brood size are eliminated.

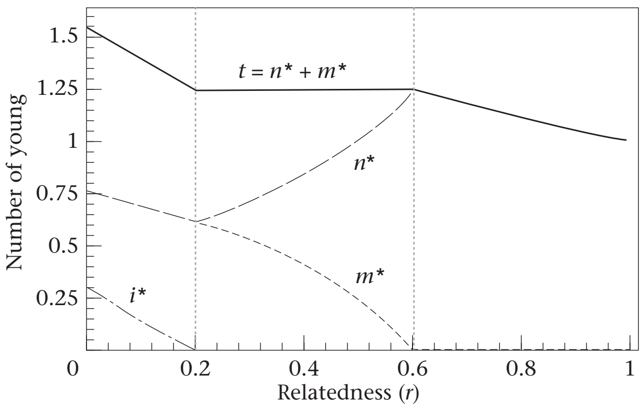

Figure 1. Stable numbers of offspring produced by Alpha (n^*) and by Beta (m^*), resulting total brood size ($t=n^*+m^*$) and number of offspring eliminated (i^*), as a function of relatedness (r), when k (the rate at which offspring survival declines with increasing brood size) equals 0.4 and μ (the cost of offspring production) equals 0.2. The vertical grey lines (at r=0.2 and r=0.6) divide the plot into three regions as described in the text.

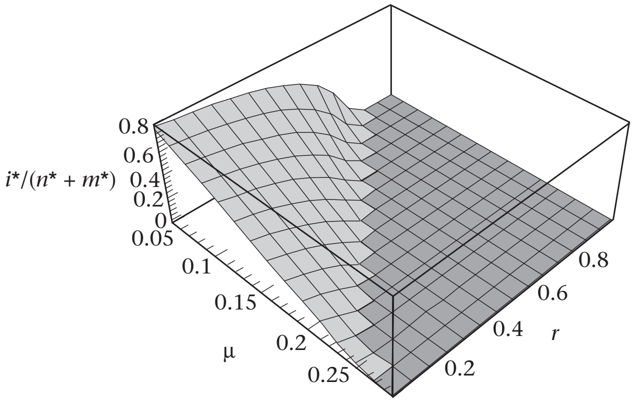

Figure 2. Proportion of the total brood that are killed at equilibrium ($i^*/[n^*+m^*]$), as a function of relatedness (r) and the cost of offspring production (μ).

Figures 2–4 summarize the effects of the model's three parameters, r, k and μ, on the evolutionarily stable outcome. Figure 2 shows the proportion of the total brood that are killed at equilibrium, as a function of r and μ (note that this proportion is not influenced by k). It reveals that high levels of infanticide are more likely when breeders are less closely related and offspring are cheap to produce.

Figure 3, which shows total brood size prior to any infanticide ($t=n^*+m^*$), again as a function of r and μ, reveals that infanticide is also associated with elevated levels of offspring production. Unsurprisingly, k also affects the equilibrium value of t, although this is not shown in the figure. The more rapidly fitness declines

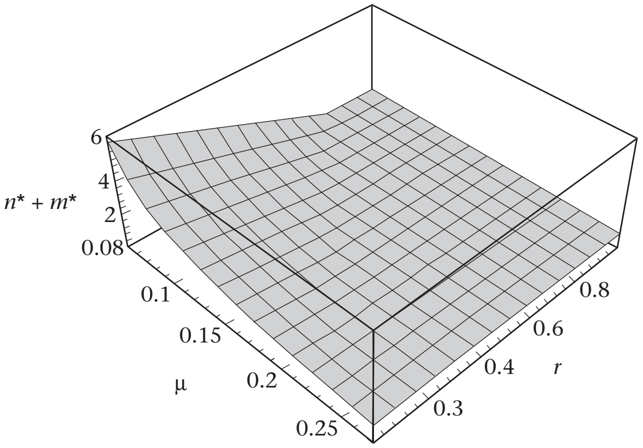

Figure 3. Total brood size at equilibrium prior to any infanticide (n^*+m^*), as a function of relatedness (r) and the cost of offspring production (μ), for k=0.4.

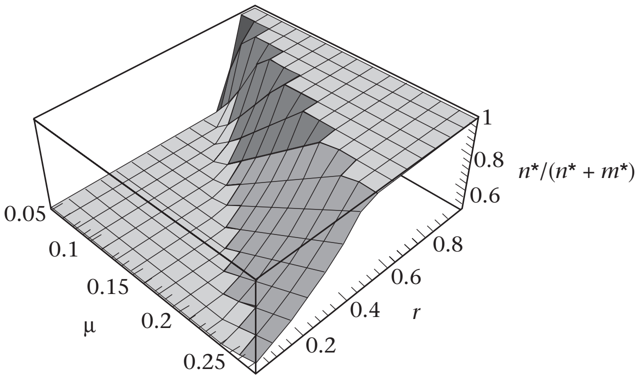

Figure 4. Stable level of skew, measured as the proportion of the total brood produced by Alpha, as a function of relatedness (r) and the cost of offspring production (μ). A value of 1 indicates that Alpha entirely monopolizes reproduction, a value of 0.5 that both breeders obtain an equal share.

with brood size (i.e. the greater the value of k), the smaller the total number of young produced.

Figure 4 shows the level of reproductive skew, measured as the share of total reproduction obtained by Alpha, as a function of r and μ (note that skew is not influenced by k). The division of reproduction is most uneven when relatedness is high and offspring are costly. Conversely, low levels of relatedness and low costs of offspring production, the circumstances that favour infanticide, also favour low levels of skew. As mentioned above, when infanticide is actually stable, Alpha and Beta produce equal numbers of offspring and obtain equal shares of the total brood.

The reason for the above result is that infanticide reduces the need for reproductive restraint on the part of Beta. Initially, at the original equilibrium calculated by Cant (1998), both breeders often stand to gain by eliminating some offspring. Once the possibility of infanticide is introduced, however, production of young by Beta no longer leads to a drop in overall brood productivity, as it did in the original model, because any young in excess of the most productive brood size will simply be eliminated. Beta can thus afford to produce more offspring, so as to claim a greater share of overall reproduction (i.e. to reduce the level of skew). The ultimate result is that Alpha suffers a loss of inclusive fitness compared with the situation where infanticide is not possible, while Beta enjoys a concomitant gain, as shown in Fig. 5.

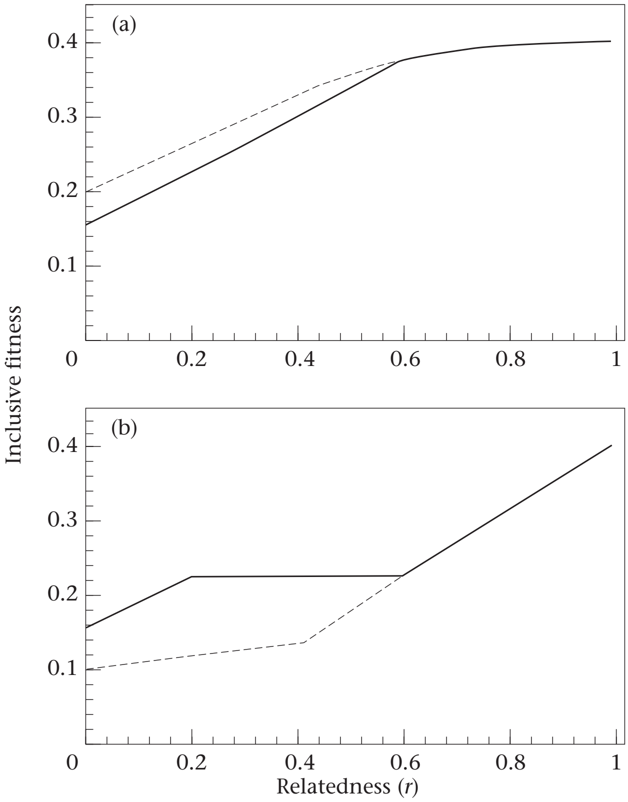

Figure 5. Inclusive fitness of (a) Alpha (the dominant individual) and (b) Beta (the subordinate), as a function of relatedness between the two (r), when the possibility of infanticide is incorporated in the model (——) and where it is not (– – –). Other parameter values used to generate the figure are k=0.4 and μ=0.2.

DISCUSSION

The chief consequence of infanticide in the model is to release Beta (the subordinate breeder) from the reproductive restraint she would otherwise be forced to exercise. When infanticide is possible, addition of numerous young to the joint brood will not lower overall productivity during the current breeding attempt, because progeny in excess of the most productive size are eliminated (although overproduction of young that are subsequently killed does entail a fitness cost to the parent). Beta is thus free to claim a larger share of the brood than would otherwise be the case, to her advantage but to Alpha's detriment (see Fig. 5). We thus predict that in societies featuring indiscriminate infanticide, reproduction will be fairly evenly distributed (although some differences between the reproductive shares of dominants and subordinates may arise owing to differences in the cost of producing offspring or in their survival chances, factors that were not addressed in the present model). In the cannibalistic ant *L. acervorum* mentioned in the Introduction (Bourke 1991, 1994), this does indeed seem to be the case. Further tests of the prediction, however, are clearly needed.

Although indiscriminate infanticide cannot directly alter the level of reproductive skew after offspring are produced (since young will be destroyed at random), the above result indicates that it may do so indirectly through its influence on the reproductive behaviour of group members. This is true even when infanticide does not occur at equilibrium. Over a part of its parameter range, the model predicts that the (unrealized) possibility of infanticide is sufficient to limit production of young by Alpha, thus restricting total brood size to the most productive level. This result supports the suggestion of Hrdy & Hausfater (1984) that aspects of social behaviour (such as spontaneous abortion) may reflect the selective pressures exerted by infanticidal acts that have 'not yet occurred and which will rarely ever be seen'.

When indiscriminate infanticide does occur, the model predicts that it will be associated with elevated production of young. Moreover, it is most likely to prove stable when the coefficient of relatedness between cobreeders is low and offspring are cheap to produce. Production of excess young, a proportion of whom will later be eliminated, is a means to skew the composition of the final brood (i.e. those offspring that are left after infanticide has occurred) further in favour of the parent. The benefits to be gained by doing so are greater when cobreeders are less closely related, because a parent's own offspring are then more valuable to her than are the progeny of her cobreeder. Equally, the costs involved are lower the cheaper offspring are to produce.

The above result suggests that indiscriminate destruction of young may typically be restricted to invertebrates (e.g. Bourke, 1991, 1994), because parental investment in individual offspring tends to be greater among vertebrates. When offspring are costly to produce, the risk of destroying one's own progeny is likely to restrict infanticide to situations in which an individual can reliably identify offspring as those of cobreeders. Koenig et al. (1995), for instance, found that while joint-nesting female acorn woodpeckers, *Melanerpes formicivorus*, often destroy eggs, this behaviour ceases when cobreeders lay simultaneously in the shared nest cavity and discrimination is no longer possible (and see also Vehrencamp et al. 1988).

How difficult is discrimination usually likely to be? As pointed out in the Introduction, spatial and temporal cues that are employed to identify young in other cases may be of little use in communal breeders, where offspring of different parents are reared together in the group. The extent to which this is the case, however, will depend upon the reproductive biology of the species in question. In honeybees, stingless bees and vespine wasps, for example, eggs are typically laid in individual cells, which may make recognition easier than among ants, where multiple queens contribute eggs to mixed heaps (A. Bourke, personal communication). An essential consideration may also be the extent to which offspring themselves stand to gain or lose by revealing or concealing their identity. Genes expressed in juveniles that produce distinctive or generic signature traits will make it easier or harder, respectively, for parents to identify their own progeny, and thus facilitate or constrain the evolution of infanticide (see Beecher 1991; Johnstone 1997; Sherman et al. 1997). The fact that there is currently no good evidence for within-group discrimination of kin classes based on genetic cues (see Keller 1997) suggests that selection for generic signatures may be common.

Although we have focused solely on the issue of indiscriminate killing, it would be of great intrest to extend the model to allow for imperfect but better-than-random discrimination (the case of perfect discrimination is of little interest: when Alpha can destroy any offspring that Beta produces, she is able to monopolize breeding, while Beta does best to refrain from any reproduction). When some discrimination is possible, it may pay a breeder to reduce total brood size below the most productive level, in order to skew the partitioning of the remaining brood further in its own favour. Under these circumstances, however, the optimal level of infanticide may differ for Alpha and for Beta, in addition to which each would obviously prefer to eliminate the other's young. Similar conflicts also arise where an individual who commits infanticide gains substantial trophic benefits from consuming the young that are destroyed. Perhaps the simplest approach that future analyses might take is thus to consider the case in which only the dominant, Alpha, can engage in the destruction of offspring.

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