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Reproductive skew and individual strategies: infanticide or cooperation?

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Abstract Infanticide in species with shared reproduction may indicate attempts to control the degree of skew within groups. Alternatively, individuals that have done poorly in reproduction could use infanticide for hastening the next breeding attempt. Many factors influence the individual's decision over whether it is best to cooperate or engage in destruction. We present a qualitative model incorporating kinship among adults and progeny, social status, group size and seasonality to predict behavioural options for individuals of diverse backgrounds. The social system used for the model was that of the guira cuckoo (*Guira guira*), a Neotropical bird that breeds communally. We suggest communal breeders utilise the best available predictors for enhancing seasonal reproductive success, with favourable consequences for lifetime inclusive fitness. Predictors rely upon parameters that change over time, including the individual's assessment of present and future possibilities. The model produces predictions that may be tested through field observations and molecular analyses for species with similar social dynamics.

Keywords Reproductive skew · Communal breeding · Infanticide · Cooperation · *Guira guira* · Guira cuckoo · Ovicide

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Introduction

For more than a decade, considerable effort has been directed towards understanding the distribution of reproductive opportunities for individuals living in groups. Optimal skew models, also called concession models (Clutton-Brock 1998), assume that dominants exert control over reproduction and will attempt to skew reproduction to the maximum degree, while the subordinate's only option would be to leave the group and attempt independent breeding (Emlen 1982, 1995; Keller and Reeve 1994; Reeve 1991, 1998; Reeve and Ratnieks 1993; Vehrencamp 1983). The degree to which dominants can reduce the subordinate's direct reproduction is greatly dictated by the harshness of ecological conditions, which may or may not favour dispersal by subordinates.

However, the assumptions of these classical models may not always hold (Clutton-Brock 1998), and either dominants may have only limited control over subordinate reproduction, or subordinates may have options other than leaving the group. For example, Johnstone and Cant (1999) suggest that when dominants are unable to prevent subordinate reproduction, dominant fitness may decrease, and they are left with only one alternative, which is to forcibly eject or exclude subordinates from the group. In support of this perspective, Johnstone and Cant (1999) cite several species of birds, mammals and fish where this may occur.

Another possibility that has not been explored in reproductive skew models includes cases where dominant control is circumvented by social strategies, leading to societies that are more egalitarian. For example, primates may form coalitions to undermine dominant control (e.g. chacma baboons *Papio cynocephalus ursinus*, Palombit et al. 2000), or females in multi-member groups may favour subordinate over dominant matings (e.g. banded mongooses *Mungos mungo*, Cant 2000). Strategic infanticide, as a form of destroying the whole brood/litter to force a new reproductive attempt, is a new option we propose. Infanticide is a fairly widespread practice, although it appears to be more common in social animals. Infanticide by males to increase reproductive success is a common phenomenon in

some groups of animals, notably primates, carnivores and rodents (reviewed in van Schaik and Janson 2000). It has also been well documented for insects (Turillazz and Cervo 1994) and birds. In the latter, this can take the form of ovicide (e.g. house sparrows *Passer domesticus*, Veiga 1993; boobies *Sula neboouxii*, Osorio-Beristain and Drummond 2001; anis *Crotophaga sulcirostris* and *Crotophaga ani*, Vehrencamp 1977; Loflin 1983; Quinn and Startek-Foote 2000; acorn woodpeckers *Melanerpes formicivorus*, Mumme et al. 1983; ostriches *Struthio camelus*, Bertram 1979; cattle egrets *Bubulcus ibis*, Fujioka 1986; great reed warblers, Hansson et al. 1997 and guira cuckoos, Davis 1940a). After hatching, adults also kill nestlings to obtain reproductive advantages (e.g. house sparrows, Veiga 1993; possibly, acorn woodpeckers, Stacey and Edwards 1983; northern jacanas *Jacana spinosa*, Stephens 1982; tropical house wrens *Troglodytes aedon*, Freed 1986; cattle egrets, Fujioka 1986 and guira cuckoos, Macedo and Melo 1999). Females committed much of the ovicide and nestling killings observed in the species listed above.

In this paper we explore the influence of an individual's social, genetic and ecological circumstances on its propensity for "cooperative" or "uncooperative" behaviour within a current breeding attempt. In particular, we elucidate the conditions where an individual may gain from committing infanticide (more specifically in the model, chick killing) to hasten the onset of another breeding attempt. The model was inspired by the guira cuckoo breeding system, from which we drew data to guide the choice of values for some parameters, but may be applied to other species where infanticide is regularly practised.

Guira cuckoos and anis (Crotophaginae, Cuculidae) exhibit highly competitive behaviours during nesting. Groove-billed anis perform ovicide through egg ejection (Vehrencamp 1977), while in smooth-billed anis, ovicide involves both egg ejection and egg burial (beneath nesting material) (Davis 1940b; Loflin 1983), and in guira cuckoos, both ovicide and infanticide after hatching are prevalent (Macedo and Bianchi 1997; Macedo and Melo 1999). Guira cuckoos inhabit savannah areas in South America, and reproductive groups occur with as many as 13 adults sharing a nest. The gross communal clutch, which correlates with group size, varies from 4 to 24 eggs. Thus, in guira cuckoos, within-group reproductive suppression may be very weak, although genetic analysis would be necessary to accurately assess this, as well as reproductive skew.

Egg ejection usually starts with the laying of the first egg and may continue for a prolonged duration, sometimes well into incubation, resulting in total collapse of the group's nesting attempt. In 215 nesting events monitored to date, 42 (19.5%) of the groups discontinued the reproductive attempt because all of the eggs were ejected. Reproductive conflict often continues after chicks hatch, with severe abridgements of most broods during the first week (Macedo and Melo 1999; Macedo et al. 2001). In 44 (63.8%) of the 69 nests where hatching occurred, the brood was subsequently reduced by a few nestlings. And in 19 (27.5%) cases, the whole brood was eliminated. These infanticidal events differ markedly from typical predator attacks. In the former,

chicks disappear sequentially (or may be found dead under the nesting tree), and there is no damage to the nest structure. In predation, generally all chicks disappear simultaneously, and the nest suffers considerable damage. Many groups can re-nest as many as five times within a single rainy season (Melo 1997), and re-nestings occur more promptly when the group's reproductive effort fails than when nestlings survive from a previous attempt (Macedo 1992).

The guira cuckoo social system exhibits a high level of complexity and variability and may be characterised by the following elements (Macedo and Bianchi 1997; Macedo et al. 2004a,b; Macedo and Melo 1999; Quinn et al. 1994): (1) reproduction is not monopolised by a single reproductive pair; (2) groups may contain several members of both sexes; (3) up to seven females may lay eggs in a nest; (4) females appear to vary their investment in eggs according to their social context; (5) groups usually, but not always, contain relatives; (4) the mating system includes polygyny and polyandry; (5) ecological constraints (e.g. habitat available for breeding) are not severe and (6) infanticide is frequently practised by group members.

A stochastic contingencies model

The model we propose is grounded upon the premises that this social system is characterised by low or moderate reproductive skew. No individual controls reproduction directly; instead, each employs selfish strategies to enhance its own reproductive success. Individuals may hold higher or lower ranking positions within the group for different tenures. The model specifically assumes that rank (or condition) of an individual may be highly variable among breeding attempts of the group, but that over the short-term (e.g. the next breeding attempt), individuals can predict their rank/condition. While we have no direct evidence that a behavioural dominance hierarchy occurs and actually changes over repeated breeding attempts, we do know that the order of entrance of females into the laying sequence of the communal nest changes with each breeding attempt, and thereby the chances of being victimized through egg ejection or having incubated eggs in the final communal clutch. It has also been shown that females in the group do not participate in all of the nesting bouts, therefore suggesting that rank and condition may translate into breeding slots in each reproductive event. We speculate that females that have participated in a nesting event may suffer some deterioration in condition, especially when laying a large number of eggs that are subjected to continuous ejection, and this may limit female participation in sequential nesting events of the group.

In this context, factors such as age, experience and physical condition could affect the number of eggs laid and order of entering the laying sequence (hence probability of egg ejection). Thus, an individual's status could change abruptly or more slowly over time, and relative reproductive success could vary within groups from one nesting attempt to another. As in classical optimal skew models, individuals can leave the group if they find themselves in a

low-ranking position for prolonged periods; but additionally, they can also use infanticide to produce nest failure, thus shortening the interval between sequential group nestings. In fact, any individual, whether of low or high status, could use infanticide to promote better reproductive prospects in the future. Infanticide, in the model's context, does not imply that individuals can recognise their own young. Rather, individuals can assess their relative reproductive success in a nest indirectly (e.g. through the number of matings, timing and quantity of eggs laid, etc.) and also predicate their own success in future nests by their present status within the group.

The mathematical argument that follows includes stochastic contingencies that would influence individuals in distinct ways, allowing an assessment of which adults in a given group are more likely to commit infanticide. The simple argument compares two measures of fitness for any chosen individual: (1) the inclusive fitness obtained at a given nesting bout and (2) the inclusive fitness the individual can expect in the group's subsequent nesting bout. When the outcome of this comparison is positive (i.e. the first quantity is larger), the individual is more likely to behave cooperatively. When the second quantity exceeds

the first, uncooperative behaviour (including infanticide) may prevail. The parameters used in the argument are given in Table 1.

The inclusive fitness of an individual at a given nesting bout is shown by Eq. (1)

$$F(A, t_i) = \sum_{j=1}^M r_j \text{ in time } t_i \quad (1)$$

where A is the adult for which the cooperation–infanticide model is being applied, and t_i indicates the occasion of the nesting bout (here we designate t_1 as present nesting bout). The inclusive fitness thus equals the sum of all r_j , denoting the coefficient of relatedness between the focal adult and each of M nestlings of that nesting bout. The communal young may include the individual's own offspring, those of related group members, or they may all be completely unrelated to the focal individual.

The inclusive fitness that the focal individual can expect in the next nesting opportunity is given by the equation:

$$E(A, t_{i+1}) = \left[\frac{\sum_{i=0}^T \frac{F(A, t_{-i})}{M_{-i}} \times (1 - e^{i-T})}{\sum_{i=0}^T (1 - e^{i-T})} \times f(g(t_1, N_1)) \times s \right] \times S. \quad (2)$$

Table 1 Parameters used in the cooperation–infanticide value model

Parameter	Definition
F	Inclusive fitness at a given nest
A	Focal adult for which CIV function is being evaluated
t_i	Occasion of nesting bout, t_0 =previous, t_1 =present and t_2 =upcoming nesting bouts, respectively
r	Coefficient of relatedness between focal adult and communal nestlings
M	Number of fledglings in a nest
E	Expected fitness at a given nest in the next reproductive attempt
T	Number of previous nesting attempts being considered in the individual's history
f	Relation between number of adults in a group and number of hatchlings
g	Probable number of adults in a next nesting bout, based upon number of present group members
N	Number of adults in a given group
s	Probability of a hatchling surviving to fledge
S	Probability of adult survival between successive nesting attempts

This equation uses a series of circumstantial parameters of the bird's present situation in the group, which include its hierarchical status (indicated by reproductive performance during past nesting events), relatedness to communal young in past nestings and size of the group at present. In Eq. (2) the formula:

$$\frac{\sum_{i=0}^T \frac{F(A, t_{-i})}{M_{-i}} \times (1 - e^{i-T})}{\sum_{i=0}^T (1 - e^{i-T})} \quad (3)$$

estimates the bird's past reproductive success within the group, thus denoting its present hierarchical status. This measure can be used as an indicator of expected future success. The numerator has two terms. The F/M quantity is the average inclusive fitness for a past period, with respect to all surviving nestlings. The $(1 - e^{i-T})$ term reduces the importance of nesting bouts farther in the past and places more weight on how the individual did in more recent bouts. The denominator in Eq. (3) is the summation of the weights needed for obtaining the weighted average of fitness over the past T nesting bouts. Thus, Eq. (3)

calculates the weighted average past reproductive success of the bird, favouring the more recent bouts preceding the present one. This increased weight was considered important because a bird may have as many as five reproductive opportunities to breed in a single reproductive season, through which its hierarchical position could change dramatically.

The function $f(g(t_1, N_1))$ in Eq. (2) designates the relationship between the number of adults in a group and the number of eggs that hatch. Field evidence to date for guira cuckoos indicates that there is a significant, positive, linear correlation between these two variables ($r_1=0.44$, $P<0.001$, $N=151$), and a regression analysis indicates that group size significantly affects initial brood size ($F_s=6.16$, $df=1$, $P=0.02$, $N=71$).

This function determines the average number of communal nestlings that will hatch, a number that is dependent upon both the number of adults in the group (as noted above) and the timing within the reproductive season. This can be better estimated by calculating the probable number of adults that will participate in the next nesting event, which is given by the function $g(t_1, N_1)$ in Eq. (2) and explained below:

$$g(t, N) = \sum_{i=1}^k p_i n_i, \text{ in occasion } t. \quad (4)$$

Occasion t designates a given period within the reproductive season. The value of Eq. (4) is generated by means of a probability function, dependent upon the number of adults in the present group. Thus $g(t, N)$ predicts the number of adults in the next nesting bout, where g is a function of t , the occasion in which a nesting bout occurs relative to the rainy season, and N is the number of adults in the current group. This quantity is given by the sum of all $p_i n_i$, where p_i represents the probability that the group will be of size n_i , in occasion t of the reproductive season. For each t and N , there exists a series of p_i where

$$\sum_{i=1}^k p_i = 1 \text{ and } 0 \leq p_i \leq 1 \text{ for all } i. \quad (5)$$

This defines a discrete probability function. In the “Appendix” we use field data from six reproductive seasons of the guira cuckoo (Table 2) to demonstrate how this part of the equation can be calculated.

The number of adults in the present breeding unit constitutes an important variable affecting the fitness expectations of group members, as this may alter the relative positioning of females in the laying sequence and even the number of breeding bouts attempted by the group. For all nesting events of the guira cuckoos recorded to date, in addition to the significant correlation to clutch size, group size also was significantly correlated with number of ejected eggs ($r_1=0.29$, $P=0.001$, $N=144$) and number of

Table 2 Calculation of p_i for all guira cuckoo groups initiating with six adult members in September or October (early reproductive season) from six reproductive seasons in the period 1987 to 1997, in Brasilia, Brazil

Number of groups found with six members (G_i)	Number of adults in re-nesting (n_i)	p_i
0	1	0
0	2	0
1	3	0.125
0	4	0
1	5	0.125
3	6	0.375
0	7	0
1	8	0.125
0	9	0
0	10	0
1	11	0.125
1	12	0.125

Total, eight groups with six members re-nested with group sizes shown in column two

chicks that hatched ($r_1=0.29$, $P=0.02$, $N=71$). Thus, despite egg ejection losses, increasing group size was associated with a higher number of hatchlings. However, larger groups were not positively associated with the number of chicks that actually fledged ($r_1=0.17$, $P=0.15$, $N=71$). Thus, infanticide (and some predation) limits the positive effects that a larger group could have in successfully fledging more chicks. Assuming that there is no recognition of offspring, an individual can presumably improve reproductive success by increasing the proportion of its own eggs incubated in each communal clutch.

A third factor, s (within the brackets of Eq. (2)), plays a significant role in determining the bird’s expected reproductive output, which is the probability of hatchling survival to fledging. This may be affected by the timing of nesting and incorporates the cost of delaying reproduction. For guira cuckoos, chick mortality may increase at the end of the rainy season (when insect abundance declines) and as a function of group composition and/or size. Thus, hatchling survival may decrease if group reproduction is overly delayed. A population index can be used for species with homogeneous social/environmental impacting factors, whereas a more refined value can be calculated (e.g., a within-group s value) for species where nestling mortality is less homogeneous across the population.

One last factor that has to be considered in predicting an individual’s success at the next nesting bout is S , the chances of adult survival between successive nesting bouts. The cost of delaying reproduction, for example, will be affected by the value of S . For older individuals or ones in poor health, there will be a greater cost to committing infanticide and delaying reproduction of the group, since their chances of survival until the next breeding attempt are lower than for young and robust individuals. Again, one

can use a general population index or a more refined value, reflecting, for instance, differential mortality between the sexes or age-specific mortality.

The two measures of inclusive fitness (present and expected) are then compared to yield the Cooperation–Infanticide Value (CIV), a qualitative index that expresses the degree of cooperative vs destructive behaviour that can be expected for each individual in a group. The CIV varies as a function of A , the focal adult, and of the time t_i within the reproductive season Eq. (6).

$$CIV(A, t_i) = F(A, t_i) - E(A, t_{i+1}) \quad (6)$$

The model can be presented verbally through the arguments that follow. CIV values are highly individualised and represent a relative quantity dependent upon the values of others in the group and will change over an individual's lifetime. It shows whether individuals are more or less predisposed to cooperate in comparison with others. Positive CIVs imply that the current nesting bout is more valuable, in terms of inclusive fitness payoffs for the individual, than what it should expect from the next nesting bout. Examples include such occasions where a presently low status breeder had few of its eggs ejected from the nest. However, because its present low social rank probably would not change much from one nesting bout to the one following immediately, the expectation of a repeated success would not be great. Another possibility would be that in which the present clutch occurred late in the rainy season, with dim prospects for another bout during this same breeding period. The higher the CIV, therefore, the more valuable the current nest and, one would generally predict, the more cooperative the individual.

Negative CIVs indicate poor fitness gains in the present bout, as compared to expectations for the next nesting event. Such circumstances could occur in cases where a presently high status individual was unsuccessful, for example, due to low mating success. This bird's high status may continue into the next nesting event, with expectations of a much better situation for the individual. Depending on how negative the CIV, we can predict a low degree of cooperation, and perhaps even infanticide, to hasten the arrival of the next breeding opportunity.

When the CIV is neutral, that is, equal to or very close to 0, cooperative behaviour could be favoured in two different contexts. First, a low status individual with few fitness payoffs in both the current nest and the next nesting bout

might find cooperation to be a good option, provided certain rewards exist. Such payoffs may include opportunities to gain parenting experience, improved chances for remaining in the group and/or increased status within the group's hierarchy. Alternatively, a neutral CIV might facilitate individual cooperation through quite a different route, such as when a high-ranking individual has high fitness gains in the current brood and high expectations for the subsequent bout as well. In this case, the fitness payoffs may be nearly identical, and parenting behaviour (e.g. cooperation) should be in the birds' own best interest.

Varying individual social rank

Various factors may contribute unevenly to the decision-making process. To envision a few possibilities, here we present some plausible although simplified sketches. In all simulations, for simplicity, we maintained the survival factor for both adults (S) and nestlings (s) equivalent to unity.

In these first simulations, we vary individual social ranking within the group (measured in terms of fitness in past nesting bouts) to assess how this factor may affect individual decisions to cooperate or act aggressively towards nestlings. We concerned ourselves with four distinct possibilities in terms of possible changes in an individual's social rank within the group, arbitrarily using seven consecutive nesting bouts and assigning fitness values to determine the following conditions: (1) individual in social ascension; (2) individual in social decline; (3) low status individual with temporary social ascension (low/high/low) and (4) high status individual with temporary social decline (high/low/high). For guira cuckoos, we may define the social ranking of a male as equivalent to his access to females (through dominance interactions) and, for females, as equivalent to the number of eggs that survives the ejection process. For these simulations, we fixed group size at six adults and used a brood size of six chicks in all nesting bouts. The outcomes depend upon what these yield when incorporated into the CIV equation Eq. (6).

Individual in social ascension or decline

Using the above parameters, and for an individual in social ascension, we fixed fitness in previous nesting bouts, t_{-4} to

Table 3 Simulation fitness values used for varying individual social condition within the group and resulting CIV values, where $T=5$, group size=6 and brood size=6 (all past and future nesting bouts)

Social condition	Fitness values (F) at					CIV values at			
	t_{-4} to t_{-2}	t_{-1}	t_0	t_1	t_2	t_{-1}	t_0	t_1	t_2
Ascension	3.0	3.0	5.0	5.5	6.0	0	2.0	1.72	1.32
Decline	3.0	3.0	1.0	0.5	0	0	-2.0	-1.72	-1.32
Low>High>Low	0.5	4.0	0.5	0.5	0.5	3.5	-1.36	-1.24	-0.90
High>Low>High	4.0	0.5	4.0	4.0	4.0	-3.5	1.36	1.24	0.90

Present nesting bout is designated as t_1

t_{-1} at 3.0 (Table 3; Fig. 1), which yields a CIV=0 for t_{-1} . The individual in social ascension has an increase in fitness at t_0 , when its CIV leaps from 0 to 2, and then declines slightly at the current nesting bout t_1 and subsequent bout t_2 , despite the fact that its fitness at that point is still ascending. The behavioural interpretation of the model using these parameters is that this bird, before its social ascension, could not be optimistic for the immediate future. This “reproductive pessimism” is based on the bird’s recent past nestings (t_{-4} to t_{-1}) of low reproductive performance. Following its fitness leap at t_0 , with the associated high CIV, a slow decline in CIV follows, due to the continuous incorporation of high fitness values into the equation used to calculate the CIV for the next nesting bout. If the bird maintains its high status in the following nesting bouts, its CIV will decline and stabilise at 0, indicating neutrality, that is, the next nesting bout has the same fitness value as the previous one. Since the stability of its CIV occurred through high, repeated fitness values, the bird’s behaviour should become constant at cooperative levels.

If this same hypothetical individual was to suffer a social decline, with fitness in previous nesting bouts the same as those used for the socially ascending bird, at t_{-1} , its CIV value will also be 0 (Table 3; Fig. 1). This individual suffers a decrease in fitness at t_0 , and its CIV falls to -2.0 , and then ascends slightly. The interpretation follows an inverse pattern of that for the individual in social ascension. As its fitness declines, the bird should become less cooperative, because its fitness in previous nesting bouts was considerably higher, and it could expect its present decline to be temporary. In other words, because it had a recent past of

more success than the present, and may expect the immediate future to match its stable and fortuitous past, its interest should be to terminate any current bouts where it is unsuccessful. The fluctuation in CIV will depend on its ongoing fitness history. However, should its subordinate status and low fitness be maintained in successive nestings, its CIV will stabilise at 0, indicating neutrality. This individual, which has nothing to gain or lose in successive nesting bouts, should be either indifferent to the brood or should cooperate if it can gain other social benefits by doing so (e.g. acquire parenting experience, social acceptance, predator protection within the territory, etc.).

Individuals with temporary social ascension or decline

To simulate ephemeral conditions in social rank, we established individuals of either low or high status with a single nesting bout of high or low success, respectively (Table 3). For a low status individual, we determined low fitness values of 0.5 for three consecutive nesting bouts (t_{-4} , t_{-3} and t_{-2}), followed by an ephemeral high fitness value at t_{-1} , then returning to low fitness values for the next three consecutive nestings. This pattern of a brief event of high reproductive success, given the past history of reproductive subordination, produces a CIV curve that peaks coincidentally with the brief event where the low status individual was reproductively very successful, and then declines to negative values (Table 3; Fig. 2). This is to be expected, considering that a low status bird should act as cooperatively as possible during the event where it is successful, since the likelihood of similar success in the

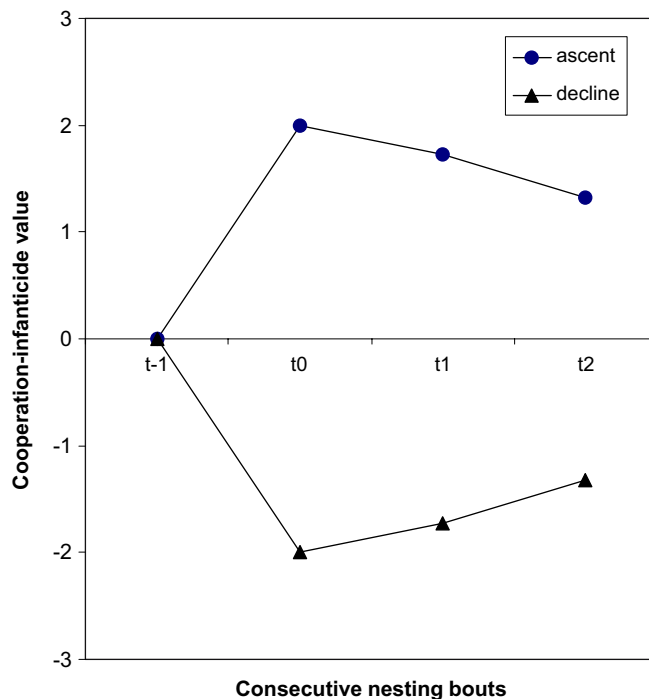


Fig. 1 Magnitude of the Cooperation–Infanticide Value (cooperation vs non-cooperation) expected as a function of social ascension or decline for four successive nesting bouts, according to fitness values shown in Table 3

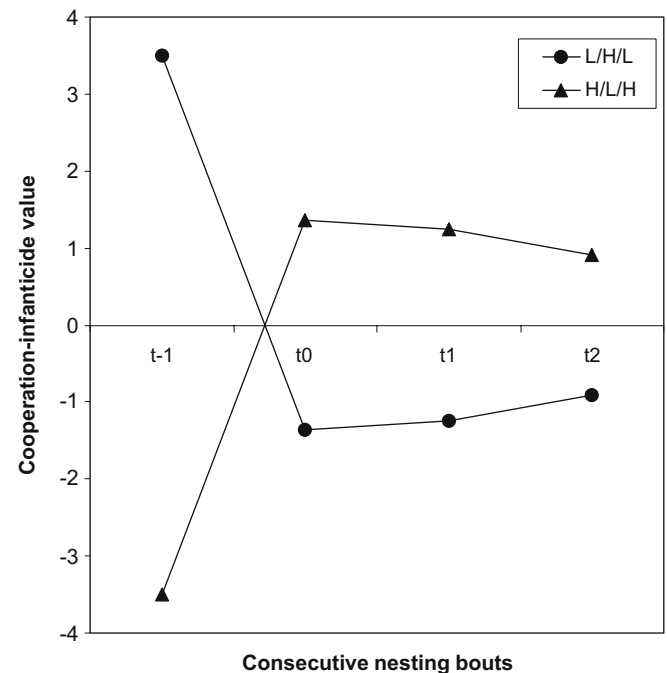


Fig. 2 Magnitude of the Cooperation–Infanticide Value (cooperation vs non-cooperation) expected as a function of sudden and ephemeral changes in social ranking for four successive nesting bouts, according to fitness values shown in Table 3

future may be small. Therefore, once its previous low status state is reinstated, its high levels of cooperation should drop off to the levels that existed prior to the brief period of high reproductive success.

We can compare this to an individual with a contrasting reproductive history, with high status held in three consecutive nesting attempts (t_{-4} , t_{-3} and t_{-2}), followed by an abrupt fall to low fitness, then returning to its previous high status. The behavioural pattern predicted by these changes in social rank is that at the point of low fitness, the individual should react by being very uncooperative (and possibly infanticidal), because poor conditions in the present nesting are not expected to become the standard. As it returns to its privileged position of high fitness, cooperative behaviour should be re-established. The slight fluctuation seen in CIV values, from t_0 to t_2 , results from the temporary decline in fitness. If these fitness reductions become cyclical through successive nesting bouts, a very gradual decline in cooperation will occur, although infanticidal behaviour would not necessarily follow. This is because once a bird enters a stage of irreversible decline in rank, each present nesting bout may actually be better than the next one. Thus, a certain level of cooperation would occur, but gradually decline as the bird's genetic representation in the brood decreases.

Varying group size

In a second set of simulations, we vary group size (which is directly related to brood size) and evaluate how these changes affect three hypothetical types of individuals that retain their status through time: high, low and intermediate. Relative to four consecutive nesting bouts, we fixed fitness values as shown in Table 4. We considered present brood size as fixed at five chicks and varied the expected brood sizes for a subsequent nesting bout. Brood size changes reflect group size changes, resulting from incoming new members, retention of offspring in the group, death or dispersal of current members, etc. All of these adjustments in the group will bring about consequences for the next breeding bout. We can then consider the differences in behaviour implied by CIV values generated for high, intermediate and low status individuals as brood size expectations vary from two to eight chicks (Table 4; Fig. 3).

When the next nesting's expected brood size decreases from five towards two chicks, the CIV for high status individuals becomes increasingly positive, at a much

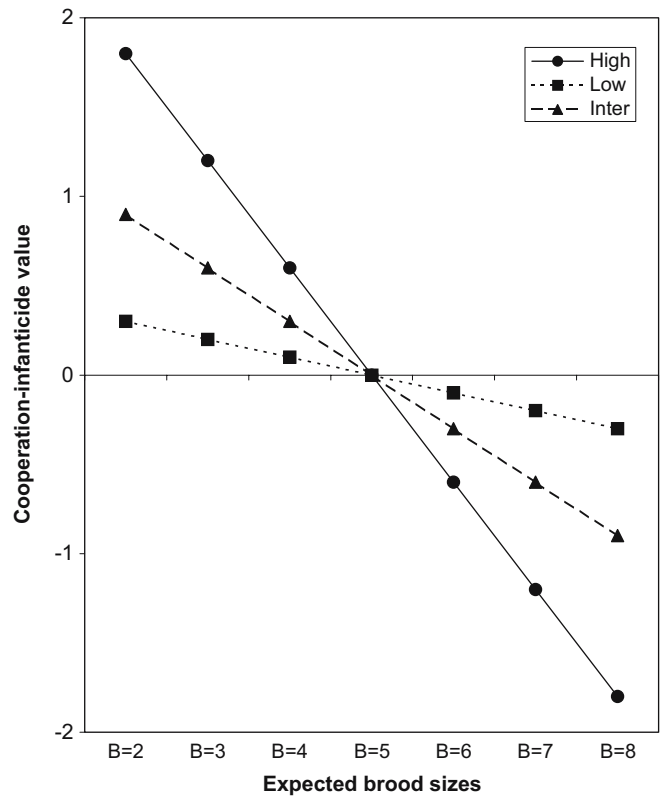


Fig. 3 Magnitude of the Cooperation–Infanticide Value (cooperation vs non-cooperation) expected as a function of expected changes in group (and therefore brood) sizes for individuals in socially high, intermediate or low ranks

steeper slope than for low and intermediate individuals. This means that, under these conditions, a high status individual that has a greater proportion of genetic representation in the brood should be extremely cooperative and protective (against infanticide) concerning the present brood (of five chicks), which it expects to be larger than the next bout's brood. If, on the other hand, expected brood size is increasing (due to increasing group sizes) and a high status individual can expect a greater fitness in a subsequent nesting bout, its CIV will drop consequently, and the individual should be less cooperative in the present nest.

In this simulation, the degree of non-cooperation and chances of becoming infanticidal will depend upon the disparity in size between the present and expected broods. For example, consider a hypothetical (although very unlikely) case of a present brood of only one chick, and

Table 4 Simulation fitness values and resulting CIV values for high, low and intermediate status individuals, when varying expected brood sizes in consecutive nesting bouts, where $T=4$ and present brood size=5

Social condition	Fitness values at t_{-4} to t_{-1}	CIV values at t_1 in expected broods of						
		2	3	4	5	6	7	8
High status	3.0	1.8	1.2	0.6	0	-0.6	-1.2	-1.8
Low status	0.5	0.3	0.2	0.1	0	-0.1	-0.2	-0.3
Intermediate status	1.5	0.9	0.6	0.3	0	-0.3	-0.6	-0.9

Present nesting bout is designated as t_1

because of an enormous change in group size, with expectations of 10 chicks for the next nesting bout. The chances of infanticidal behaviour, especially for a high status bird, would be extremely high in comparison with smaller differences between the present and the expected broods (say, four chicks in the present vs six chicks in the expected brood). Thus, a high status individual should be amenable to discrete group size increases favouring the opposite sex. For high status males, access to many mating partners would assure a greater proportion of genetic representation in a larger brood. And for high status females in a promiscuous mating system, a higher level of genetic variability within her brood might be advantageous, in addition to lowering the propensity of infanticidal males in the group. Levels of cooperation should not fluctuate greatly if brood sizes in consecutive nestings vary only slightly, as a result of small changes in group size.

The slopes of all three lines (high, intermediate and low status) indicate that expected brood size increases lead to higher expected fitness than present fitness for all types of individuals in the group, with associated declines in CIVs. Larger group sizes result in larger broods, but usually a smaller proportion of reproductive success for most individuals. Thus, increases in group size should lead to less overall “eagerness” to cooperate for all individuals, despite the fact that absolute individual fitness values will increase. When group sizes are stable from one nesting bout to another, brood sizes stabilise and cooperative behaviour (in varying degrees, depending upon the rank of the individual) ensues.

Discussion

The current vs future trade-off in reproduction, so often emphasised in life-history theory, has been neglected in most arguments about the evolution of social behaviour. Most models do not consider the dynamic individual decision-making process, which is subject at any moment to unpredictable external or internal (physiological) events. Here we suggest that, in addition to the degree of present reproductive skew within groups, individual future reproductive opportunity may be a major factor determining cooperative or destructive behaviour. Thus, for guira cuckoos and socially similar iteroparous species, inclusive fitness gains represent only one of the components that precipitates cooperative behaviour. The possibility of status changes within the group and of obtaining a larger proportion of direct reproduction in the future may be one incentive for remaining in the group and, if not cooperating, at least refraining from infanticide.

The behaviour of a social individual is not static, but rather suffers changes that incorporate the cumulative reproductive experiences of the bird as its rank shifts within the group. These changes in rank result from various factors (e.g. disease, age, nutritional condition, group size changes, sex ratio within groups, availability of mates) that impact the individual's life, whether in a larger context (through the years) or in a more restricted context (within a single

season). Levels of cooperative and uncooperative behaviours should thus be highly variable when comparing individuals within groups and should also fluctuate as we look at each individual through time. If a single individual is placed in a position where it could be better off destroying the brood/litter, the whole group will suffer the consequences. Thus, a delicate point of balance has to be achieved, where each individual maximises its own fitness while risking losing the cooperation of other group members.

Infanticide within the scope of sexual selection has been identified as a behavioural strategy to speed up sexual receptivity of females (common in primates, carnivores and rodents; reviewed in van Schaik and Janson 2000), obtain more advantageous matings in birds (Crook and Shields 1985; Hotta 1994; Veiga 1990) and secure better nests or ones in a more advanced phase of construction (Hotta 1994; Robertson and Stutchbury 1988).

However, for guira cuckoos, and over 20 other bird species with comparable communal systems (e.g. anis, acorn woodpeckers, ostriches, pukekos *Porphyrio porphyrio*, magpie geese *Anseranas semipalmata*; reviewed in Brown 1987), we propose that infanticide through egg destruction and nestling elimination (when it occurs) may serve two very different purposes. Destruction of the eggs of co-breeders may sometimes be used by individuals to skew reproduction in their favour (either directly by the ability to discriminate own eggs, or indirectly, using contextual cues). For birds that use this strategy, a cooperation threshold point apparently is reached in most nests, because egg ejection ceases, and eggs accumulate and are eventually incubated. In other cases, ovicide may be an attempt at forcing a new nesting of the group. For example, in guira cuckoos, many nests are deserted after eggs are continuously ejected (23% of 207 nesting attempts monitored to date). In some of the more extreme cases, up to 24 eggs were ejected from a nest before activity ceased.

Chick elimination may also be used in these two contexts. Partial brood elimination may be an attempt to skew reproduction, while whole brood destruction may be a “last-ditch” effort to force a re-nesting of the group. The exact circumstances where such extreme behaviour becomes attractive vary greatly among individuals. This behavioural option also changes as the bird's own circumstances change, from season to season, or even from one nesting attempt to the next.

Kin selection should generally lead to the more likely strategy of cooperation, rather than infanticide, when individuals have direct descendants in the communal brood. Deviations from this expectation are likely, however, when animals are exposed to even subtle distortions within this general framework. In this model, we proposed several specific factors, which may be perceived by the animal through cues in its physiological, social and physical environment. The individual may be able to assess its status within the group from its reproductive history, physiological state or age. These factors, in combination, may predict success in the near future. Together with extrinsic elements, such as timing within the reproductive season, these cues

may trigger behavioural responses such as feeding of nestlings at varying levels of intensity, relative indifference to them or infanticide. The model provides the basis for several predictions about social behaviour in different species, which use kin selection arguments in conjunction with other variable conditions:

Prediction 1 Cooperation is especially likely to be the strategy of choice for low status individuals that are experiencing present reproductive success in a breeding opportunity but that have poor future breeding prospects.

Prediction 2 Because high status individuals own a greater genetic proportion of the brood than do lower ranking individuals, their propensity for cooperation or infanticide (all other conditions being equal) should always be more forceful than that for individuals of lower social rank. When such individuals maintain their favourable condition through long periods, they continuously monopolise a higher proportion of breeding slots in the group. However, if by chance some unfavourable condition (e.g. death of a favoured breeding partner) leads to a current depression in fitness, such individuals could, through uncooperative or infanticidal tactics, hasten the re-establishment of their favourable condition in a next breeding attempt.

Prediction 3 Extremes in individual behaviour, such as exceptionally high rates of parental investment or infanticide, should occur in situations where there are great changes in rank and/or group size adjustments.

Prediction 4 An individual of either high or low status, without adult kin in the group and no direct descendants in the current breeding event, but that can expect successful reproduction shortly, should opt for infanticide as a reproductive strategy if the successful elimination of all communal offspring leads to a faster resumption of breeding by the group.

Prediction 5 Similarly, individuals of any status that have few or no direct descendants in the current brood may kill even their own offspring if they have reason to expect a much greater success in the next reproductive attempt. Such individuals would presumably sacrifice current, small fitness gains in favour of a much greater future expected fitness.

Even within a relatively inflexible framework of an established social system, individuals still should opt, whenever possible, for those behavioural strategies that will increase lifelong fitness. To test the predictions generated by the model in different species, long-term field work, associated with molecular genetics, is necessary to determine kinship levels, changes in social or reproductive status of individuals, group size changes, individual behaviour and mortality of adults and young.

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Appendix

In this appendix we demonstrate how a key part of the CIV equation can be calculated, under natural conditions, given known field data on guira cuckoos. The relation between the number of adults in a group and the number of eggs that hatch, $f(g(t_1, N_1))$, is one of significant correlation (Macedo 1992). This relation is used to determine the probable number of communal hatchlings that an individual can expect in the next nesting bout. To calculate the probable number of adults in the next nesting bout we use:

$$g(t, N) = \sum_{i=1}^k p_i n_i,$$

where p_i represents the probability that the group will be of size n_i in occasion t of the reproductive season. For each N and t there exists a series of p_i where:

$$\sum_{i=1}^k p_i = 1 \text{ and } 0 \leq p_i \leq 1 \text{ for all } i.$$

This defines a discrete probabilistic function.

To exemplify, below we calculate the above function under different conditions, with data obtained in six reproductive seasons between 1987 and 1997. The timing of nesting, which coincides with the beginning of the rainy season, may be classified arbitrarily in the following manner: (1) early season, July to November and (2) late season, December to April. By late March, few nests are found, as the rainy season comes to an end. For each nesting event of a group, occurring in each of the above time periods, we may determine a probable number of adults in a next nesting event by using the probabilistic function developed with data from all past events. Let us, for instance, calculate this function for the initial group size of six individuals, where group size for a subsequent nesting bout is known (see Table 2). For t = early season and $N=6$ individuals, $g(t, N)$ can be evaluated by:

$$g(\text{early season}, 6) = \sum_{i=1}^{12} p_i n_i.$$

Each p_i ($1 \leq i \leq 12$) is calculated from the Table 2 values as

$$p_i = \frac{G_i}{\sum_{i=1}^{12} G_i}.$$

For example:

$$P_3 = \frac{G_3}{\sum_{i=1}^{12} G_i} = \frac{1}{8} = 0.125.$$

Thus,

$$g(\text{early season}, 6) = (3 \times 0.125) + (5 \times 0.125) \\ + (6 \times 0.375) + (8 \times 0.125) \\ + (11 \times 0.125) + (12 \times 0.125)$$

$$g(\text{early season}, 6) = \sum_{i=1}^{12} p_i n_i = 7.13$$

where we have eliminated the terms which equal to 0. In other words, for groups in the early part of the reproductive season that start out on their first nesting bout with a group size of six individuals, the expectation is that in a subsequent nesting event, the average group size will be of 7.13 adults. By using the known correlation values for different group sizes, a corresponding number of hatchlings can be calculated. This probabilistic function can be executed, then, for all groups that re-nested and for which group sizes have been recorded.

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