The role of kin recognition in the evolution of conspecific brood parasitism

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Conspecific brood parasitism (CBP) is a common strategy in several species of birds. Currently, some studies suggest that relatedness between host and parasite enhances CBP, since indirect fitness benefits could select for acceptance of related eggs by hosts. Conversely, parasites should avoid laying eggs in nests of relatives if this is costly for the host. Based on the latter argument, kinship should not promote brood parasitism. A recent model clarified this relationship, and showed that kinship can promote brood parasitism, assuming kin recognition. However, in that model kin recognition was assumed perfect. Here we present a model that addresses the role of relatedness and kin selection in CBP, when kin recognition is not perfect and hosts do not always detect parasitism. We consider both the indirect fitness of the parasite and the possible responses of the host. Our results indicate that the existence and accuracy of a kin recognition system is crucial to the final outcome. When CBP represents a cost to the host, a parasitic female that has the choice should avoid parasitizing relatives, unless (1) the costs are not too high and (2) hosts can accurately enough recognize eggs laid by relatives, rejecting them less often than eggs laid by nonkin. But if 'parasitism' enhances the direct fitness of the host (which is possible in species with precocial young) parasites should choose relatives whenever possible, even if hosts do not recognize kin eggs.

In many bird populations females have been reported to lay eggs in nests of conspecifics who will incubate them and provide parental care. This reproductive strategy is known as egg dumping or conspecific brood parasitism (CBP). Two decades ago, only 53 species were known to show this behaviour (Yom-Tov 1980) but since then the number has risen to 236 (Yom-Tov 2001). Conspecific brood parasitism differs in one important respect from interspecific brood parasitism: host and parasite may be related. To understand the evolution of conspecific brood parasitism, it is therefore important to consider the possibility that kin selection plays a role in the evolution of CBP (Andersson & Eriksson 1982; Andersson 1984; Lyon & Eadie 2000; Andersson 2001).

Based on Hamilton's theory of kin selection (Hamilton 1964), it has been argued that genetic relatedness should reduce the disadvantage of being parasitized and there-

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fore favour acceptance of eggs by the host (Andersson & Eriksson 1982; Andersson 1984). Some studies have found support for this idea in showing that populations where parasitism is abundant show high levels of female philopatry (McRae & Burke 1996; Andersson & Åhlund 2000). However, if brood parasitism has negative consequences for the host's fitness, it seems that parasites should precisely avoid parasitizing close relatives and, thus, lay their eggs in the nests of nonrelated females in order to increase their inclusive fitness. This has been already pointed out by Zink (2000) and empirical evidence for it has been shown in two studies (Emlen & Wrege 1986; Semel & Sherman 2001). There are, then, two possible opposite answers to the same question.

However, as Lyon & Eadie (2000) noted, Andersson's (1984) and Zink's (2000) theories evaluate two different points of view. While Andersson considered the host's fitness, Zink tackled the problem from the perspective of the parasite, not considering the hosts' response to parasitism. Furthermore, in his main model Zink assumed that parasitism is highly costly for hosts. In bird species with precocial young, this is not necessarily true: if per capita predation risk is diluted with increasing brood size,

survival of young can also increase with brood size. In white-winged scoters, *Melanitta fusca deglandi*, survival of ducklings of larger broods is greater than that of small broods (Kehoe 1989). In Barrow's goldeneyes, *Bucephala islandica*, females who adopt broods do not suffer any detectable cost nor do they gain any benefit (Eadie & Lyon 1998). While these studies concern young that are adopted after incubation (and hence ignore incubation costs, Thomson et al. 1998), they highlight that it is not necessarily costly to rear extra offspring if these are precocial. Zink (2000, Appendix C) mentioned this possibility.

Thus, should one expect relatedness to promote CBP? As the decision whether to parasitize a relative or a nonrelative is made by the parasite, it is the parasite's fitness that should be taken into account in the first place. However, this fitness will depend on the host's response, that is whether she will accept or reject the parasitic eggs. Therefore, if kin selection favours the host's acceptance of genetically related eggs and rejection of nonrelated eggs, it might pay the parasite to lay her eggs in the nest of a relative who will be more likely to accept them. In a recent model, Andersson (2001) explored this question, and found that with sufficient relatedness between host and parasite and relatively low costs of parasitism, hosts should accept parasitic eggs. When related hosts accept parasitic eggs but unrelated hosts resist, it is advantageous for the parasite to choose relatives as hosts. Under this scenario, kinship can promote brood parasitism.

While Andersson's (2001) paper clearly succeeds in reconciling the two points of view, it assumes that kinship recognition is perfect: a related host's optimal behaviour is determined separately from an unrelated host's behaviour. However, kin recognition systems are likely to be imperfect (Agrawal 2001), especially if the host is not at the nest when the parasite lays eggs. The question remains, will Andersson's (2001) conclusions remain valid if recognition systems are imperfect?

Our aim is to present a simple model where we explore the conditions under which a female should lay her eggs in the nest of a close relative rather than an unrelated female, under varying assumptions about the strength of kin recognition. Our model incorporates the essence of factors considered by Zink (2000) and Andersson (2001) in their models, but is considerably simpler, which makes the results more concise and eases the interpretation regarding our central point, the effect of kin recognition. We take into consideration both the parasite's indirect fitness and a possible range of the host's responses to parasitism.

MODELLING PARASITE AND HOST BEHAVIOUR

Following Andersson & Eriksson (1982), we calculate the reproductive success of a female as the number of eggs times their probability of survival to fledging age. This probability of survival is a function of the number of eggs in the nest. Table 1 summarizes the parameters used in the model. We assume that the success of the parasite's own nest does not depend on the fate of her parasitic

Table 1. Parameters used in the model

Parameter	Description
C_O	Number of eggs laid by a nonparasitic female in a nest without parasitism ($C_O>0$)
C_P	Number of eggs laid by a parasitic female in the host's nest ($C_P>0$)
C_h	Number of eggs laid by a nonparasitic female when parasitized ($C_h>0$)
$p(C)$	Proportion of eggs that give young surviving to fledging age as a function of the total number of eggs in the nest C ($0 \leq p(C) \leq 1$)
r	Coefficient of genetic relatedness between host and parasite ($0 \leq r \leq 0.5$)
A_O	Probability of accepting eggs laid by a non-relative ($0 \leq A_O \leq 1$)
A_r	Probability of accepting eggs laid by a relative ($0 \leq A_r \leq 1$)

eggs, and this component of the parasite's fitness can hence be ignored in fitness calculations. C denotes the clutch sizes laid by the host (C_h), parasite (C_p) or non-parasitized female (C_O), and the per capita survival of an egg to fledging in a brood of total size C is $p(C)$. The direct fitness of a parasitic female (w_p), a parasitized female (w_h) and a nonparasitized female (w_O) is then

$$w_p = C_p \, p(C_h + C_p) \tag{1}$$

$$w_h = C_h \, p(C_h + C_p) \tag{2}$$

$$w_O = C_O \, p(C_O) \tag{3}$$

For simplicity we assume that the host female does not lay eggs parasitically or that, if she does, this does not affect the success of chicks in her own nest. Similarly, in equation (1) we consider only the fitness that the parasite gains by parasitic egg laying, that is we assume that the fate of parasitic eggs does not influence the success of eggs that the parasite (possibly) rears herself. This is a simplification that corresponds to setting $v_u = v_p$ in Andersson's model.

We also simplify Andersson's (2001) model by assuming just a single step of accepting or rejecting parasitism attempts. An unrelated host accepts parasitic eggs with probability A_O; a related host accepts these with probability A_r. Rejection (probability $1 - A_O$ or $1 - A_r$) can be interpreted either as the host removing the eggs from the nest, or as preventing parasitic egg laying in the first place. Optimal acceptance probabilities for the host will always equal either zero (if parasitism is harmful to the host) or one (if it is beneficial); these behaviours were derived in Andersson (2001). However, in practice, hosts will often be constrained in their actions, either because they do not detect parasitism (in which case the acceptance probability can increase from its optimum) or because kin discrimination is not complete. If hosts cannot recognize kin at all, we have a constraint $A_O = A_r$.

We next calculate the inclusive fitness of the parasite, taking into account the probability that the host accepts

Table 2. Payoff matrix for parasitic female

Host	Host rejects	Host accepts
Relative	$rC_0p(C_0)$	$C_pp(C_h+C_p)+rC_hp(C_h+C_p)$
Nonrelative	$rC_0p(C_0)$	$C_pp(C_h+C_p)+rC_0p(C_0)$

r refers to relatedness between parasite and related female, regardless of whether the host is a relative.

the eggs. The payoffs of the parasitic act can be calculated by summing the parasite's direct fitness and its indirect fitness. The direct fitness is composed of the number of eggs the parasite lays, the probability that the host accepts them, and the subsequent survival probability of accepted parasitic eggs. When the host rejects the eggs, the parasite's direct fitness is zero. The indirect fitness comprises the success (number and survival) of the related host's eggs. The parasite's success and the related host's success are calculated for two alternative cases: the parasite chooses (1) the related host, or (2) some other female. Table 2 summarizes these payoffs.

We consider two possible situations: absence and presence of kin recognition of parasitic eggs by the host.

Absence of Kin Recognition by Host

We first consider the case where hosts cannot detect parasitic eggs or females, or if they can, they cannot determine whether they are genetically related to her. Parasitized females will therefore accept eggs of a related parasite with the same probability as those of an unrelated one; we denote this probability by A_0 ($0 \leq A_0 \leq 1$). The inclusive fitness of the parasite when parasitizing a related female (W_r) or when parasitizing an unrelated one (W_u) are

$$W_r=A_0w_p+r[A_0w_h+(1-A_0)w_0]=A_0C_p\,p(C_h+C_p)$$
$$+r[A_0C_h\,p(C_h+C_p)+(1-A_0)C_0\,p(C_0)] \quad (4)$$

$$W_u=A_0w_p+rw_0=A_0C_p\,p(C_h+C_p)+rC_0\,p(C_0) \quad (5)$$

Note that in equation (5), the r refers to relatedness between parasite and related female (whom the parasite chose not to parasitize). Kin selection favours CBP if $W_r>W_u$. This holds if

$$C_h\,p(C_h+C_p)>C_0\,p(C_0) \quad (6)$$

If we assume that the total number of eggs in a parasitized nest is larger than the clutch size of a nonparasitized female (i.e. $C_p+C_h>C_0$), and that a host does not lay more eggs than she would if she were not parasitized (i.e. $C_h \leq C_0$) then equation (6) holds only when the probability of survival of eggs and hatchlings increases with clutch size. Generally, equation (6) holds when the direct fitness of a parasitized female is greater than that of an unparasitized female. Thus, for a female bird to benefit from parasitizing a relative, brood parasitism has to favour the host female directly, assuming there is no kin recognition of parasitic eggs.

Presence of Kin Recognition by Hosts

The above analysis shows that in the absence of a mechanism of kin recognition of the eggs of kin, parasitizing nonrelatives is preferable when parasitism is detrimental to the host. What happens if the host female has the ability to recognize parasitic eggs? Andersson (2001) showed that kin selection can favour host females accepting eggs from related females, but he made the rather strong assumption that kin discrimination is perfect. In the previous section, we showed that a complete lack of kin discrimination will mean that kinship cannot promote parasitism when it is costly (as also suggested by Andersson 2001). It is therefore of interest to ask, can kinship promote brood parasitism when kin recognition exists but is not perfect?

First, assume perfect kin recognition. The fitness of a host female when she accepts (W_a) and when she rejects the parasitic eggs (W_n) is

$$W_a=C_h\,p(C_h+C_p)+rC_p\,p(C_h+C_p) \quad (7)$$

$$W_n=C_0\,p(C_0) \quad (8)$$

Here the first term on the right-hand side of the equations represents the host's own fitness and the second term (equation 7) her indirect fitness through the parasite. For acceptance to benefit the host ($W_a>W_n$), relatedness has to be sufficiently high:

$$r>\frac{C_0p(C_0)-C_hp(C_h+C_p)}{C_pp(C_h+C_p)} \quad (9)$$

Therefore, acceptance can pay for a sufficiently large r even when parasitism reduces the direct fitness of the host, confirming the Andersson's (2001) result.

Next, we consider the effect of imperfect kin recognition for the cases where hosts would benefit from recognizing the eggs when laid by a relative. The optimal values of acceptance for the host would in this case be $A_r=1$ and $A_0=0$ but, because of the possibilities of not recognizing kin and not recognizing parasitism per se, we assume $A_r>A_0>0$ and phrase the question: how much larger does A_r need to be than A_0, for kinship to promote brood parasitism?

The probabilities of acceptance A_r and A_0 do not necessarily have to be the consequence of recognition of the eggs themselves. 'Rejection of eggs' can be indirectly achieved through recognition and chasing off of nonkin potential parasites from the nest before they lay the eggs.

We can now calculate the inclusive fitnesses W_r and W_u of parasites laying eggs in nests of related or unrelated females, respectively, where the probability of acceptance is A_r in the first case and A_0 in the second case. Following Table 2 we obtain:

$$W_r=A_r[C_p\,p(C_h+C_p)+rC_h\,p(C_h+C_p)]+(1-A_r)rC_0\,p(C_0) \quad (10)$$

$$W_u=A_0[C_p\,p(C_h+C_p)+rC_0\,p(C_0)]+(1-A_0)rC_0\,p(C_0) \quad (11)$$

The first term in these equations represents the parasite's fitness when the eggs are accepted while the second one represents the fitness when eggs are rejected. For the parasite to lay her eggs in the nest of the related female rather than in that of the unrelated female, W_r has to exceed W_u. This leads to the result that parasites should lay eggs in related females' nests if

$$\frac{A_r}{A_0} > \frac{C_p p(C_h + C_p)}{C_p p(C_h + C_p) + r[C_h p(C_h + C_p) - C_0 p(C_0)]}. \quad (12)$$

The previous section showed that, in the absence of kin recognition, it pays to parasitize related females if being 'parasitized' increases the direct fitness of the host. But if parasitism reduces the direct fitness of the host, $C_h p(C_h + C_p) < C_0 p(C_0)$, the right-hand side of equation (12) always exceeds 1 and increases with relatedness. The condition that favours parasitizing relatives therefore becomes stricter with increasing relatedness (Fig. 1). This is intuitively clear: parasitizing a relative is costly to the parasite if the host suffers from additional eggs, since parasitism then decreases the indirect fitness gain from the host. But increasing relatedness also means that hosts are more likely to benefit from accepting a relative's eggs (equation 9). If hosts can accurately discriminate between related and unrelated females' eggs (A_r/A_0 is large) equations (9) and (12) can be satisfied simultaneously, and relatedness then favours brood parasitism even though kin recognition is not perfect.

Figure 1 exemplifies this interaction between host and parasite behaviour. In this example the host suffers a direct cost from accepting eggs, but if relatedness $r > 0.42$, it should accept eggs because of indirect fitness benefits. Consider the case $r = 0.5$ (e.g. a mother–daughter association) for three points A, B and C (Fig. 1). At point A, kin recognition (or recognition of parasitic eggs in general) is impossible, and the host is therefore constrained to use $A_r = A_0$ (or $A_r/A_0 = 1$) even though it would benefit from kin discrimination. For the parasite, parasitizing a relative therefore brings about no direct benefit, and it induces an indirect cost via the host. The result is that the parasite should favour unrelated females as hosts. However, if kin recognition is possible, we can expect $A_r > A_0$ because hosts have an incentive to accept related eggs (since the parameter values of this example satisfy equation 9 at $r = 0.5$). Whether kinship promotes brood parasitism depends on how accurate kin recognition is, that is how large A_r/A_0 is. At point B, kin recognition is inaccurate: kin eggs are 10% more likely to be accepted than nonkin eggs. This is not a sufficiently strong benefit for parasites to favour related females as hosts (equation 12 is not fulfilled). At point C, kin eggs are 40% more likely to be accepted than nonkin eggs, and now relatedness favours brood parasitism: it is better to parasitize when it can be done in a related female's nest.

The threshold value for the accuracy of kin recognition, A_r/A_0, that has to be exceeded before relatedness starts promoting (rather than hindering) conspecific brood parasitism depends on relatedness r between host and parasite as well as on costs of parasitism to the host. Costs
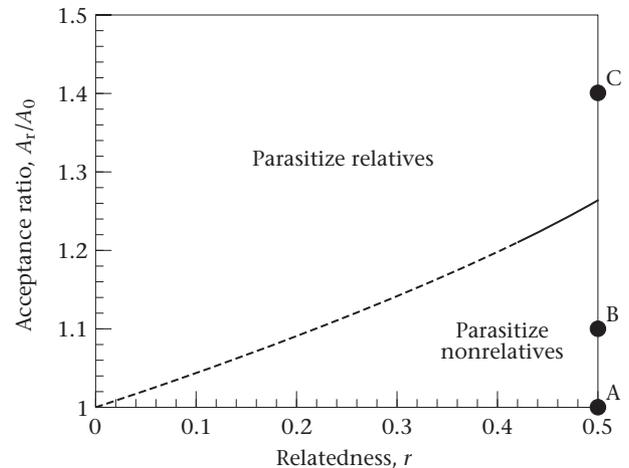

Figure 1. Optimal behaviour of the parasite, when $C_p = 2$, $C_h = 10$, $C_0 = 10$, $p(C_p + C_h) = 0.6$, and $p(C_0) = 0.65$. (See Table 1 for parameters.) Relatedness promotes conspecific brood parasitism only if related eggs are sufficiently more likely to be accepted than nonkin eggs (A_r/A_0 exceeds a threshold). The solid line indicates relatedness values for which it is beneficial for the host to accept related eggs (and A_r/A_0 values exceeding the threshold are therefore possible). The dashed line indicates that the threshold value A_r/A_0 is unlikely to be exceeded, because relatedness is so low that it does not pay for the host to accept related eggs even if kin recognition is accurate. Points A, B and C exemplify solutions where relatedness between parasite and related host equals 0.5, and hosts cannot recognize kinship of parasitic eggs (A), or this recognition is relatively inaccurate (B) or accurate (C). Kinship promotes brood parasitism only in case C.

of parasitism to the host can be either a reduction in the host's clutch size (Lyon 1998) or a reduction in nestling survival when there is an increase in the total clutch size (Andersson & Eriksson 1982). The larger the costs, the more difficult it is for a parasitic female to gain through parasitizing close relatives. The acceptance ratio (A_r/A_0) that must be exceeded increases with the direct cost to the host, and simultaneously high costs make it harder for relatedness to satisfy the condition for kin recognition to be beneficial to the host (equation 9). This applies whether costs of being parasitized are high in terms of per capita survival of chicks (Fig. 2) or the number of eggs the host can lay (Fig. 3). Thus, the larger the costs for the host, the more accurate the kin recognition system needed before kinship promotes CBP. Furthermore, if these costs are high, it is less likely that host females benefit from accepting parasitic eggs from related females in the first place (equation 9; Figs 1–3).

The value of A_r/A_0 summarizes both the effects of kin recognition (i.e. whether $A_r > A_0$) and the detection of brood parasitism per se (the absolute value of A_0). If hosts rarely detect brood parasitism, A_0 is near 1, and A_r/A_0 consequently cannot be high. In other words, if all hosts accept parasitic eggs simply because they cannot discriminate between their own and foreign eggs and do not observe egg laying by other females, kin hosts cannot offer much better prospects than nonkin hosts. In such a case, brood parasitism is favoured not because of kinship, but because of the overall high prospects of success for parasitic eggs.
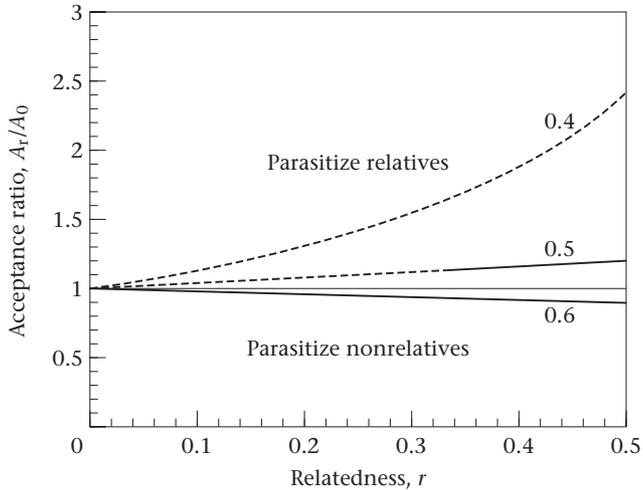
Figure 2. The threshold acceptance ratio A_r/A_0 of accepting kin versus nonkin eggs for various costs on host's fitness. The examples assume that hosts lay fewer eggs if they are parasitized ($C_h=9$, $C_0=10$), but total clutch size is larger in parasitized nests ($C_p=3$, hence $C_h+C_p>C_0$). As in Fig. 1, solid lines indicate the threshold A_r/A_0 above which kinship promotes brood parasitism, and it is beneficial for the host to accept related eggs. Dashed lines indicate a threshold that is unlikely to be exceeded because hosts do not benefit from accepting eggs. The thin solid line marks the absence of kin recognition $A_r=A_0$ (it is reasonable to assume that the true value of A_r/A_0 never falls below this line). Per capita survival $p(C_0)=0.5$ in all cases, and numbers indicate $p(C_h+C_p)$ that is either lower (0.4), equal (0.5) or higher (0.6) than $p(C_0)$. Kin recognition would have to be very strong in the first case for kinship to promote brood parasitism, but the evolution of kinship-dependent acceptance is unlikely in this case since it does not fulfil equation (9) at any value of r. When $p(C_h+C_p)=0.5$, equation (9) is fulfilled for $r>0.33$, and if kin recognition is accurate (A_r/A_0 is sufficiently high) kinship can promote brood parasitism. When $p(C_h+C_p)=0.6$, the direct fitness of the host increases if parasitized. The threshold value of A_r/A_0 (equation 12) then falls below 1, meaning that even in the absence of kin recognition ($A_r=A_0$) parasites should favour related hosts, for any value of $r>0$.

DISCUSSION

Andersson's (2001) model has made an important contribution to the understanding of the costs and benefits of using related females' nests in conspecific brood parasitism. Our findings broadly support his ideas, but add a new variable: accuracy of kin recognition systems. While Andersson assumes perfect kin recognition, we allow for it to be imperfect by setting different values of A_r and A_0. Figure 4 summarizes the results of our model.

First, when parasitism entails a direct benefit to the host, benefits of parasitism are enhanced when hosts are relatives of parasites (and kinship therefore promotes CBP). For example, if CBP causes an increase in total clutch size, it may be most favourable in precocial species, where competition among offspring is not strong and dilution of predation risk (Eadie et al. 1988) can instead increase nestling survival in large broods. In fact, CBP is more common in bird species with precocial than altricial young (Rohwer & Freeman 1989; Yom-Tov 2001). Evidence for the benefits of increased brood size in
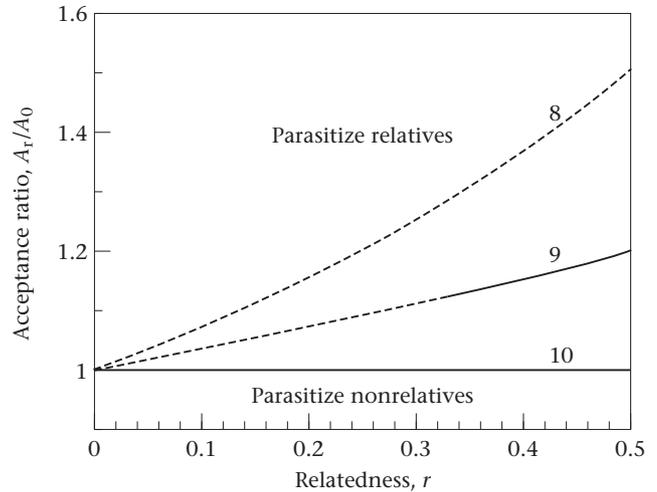

Figure 3. The threshold acceptance ratio A_r/A_0 of accepting kin versus nonkin eggs for various clutch sizes of the host as a response to parasitism: clutch size of host is $C_h=8$, 9 or 10, whereas $C_0=10$ for an unparasitized female. It is assumed that $C_p=3$, and that increasing clutch size does not affect chick survival, $p(C_0)=p(C_h+C_p)=0.6$. The larger the cost to the host (the smaller her clutch size C_h when parasitized), the more accurate kin recognition is required for kinship to promote brood parasitism, and the higher the relatedness needed before hosts should accept eggs. When costs are high ($C_h=8$), kinship-dependent acceptance probability ($A_r/A_0>1$) is unlikely to evolve at all because equation (9) is not fulfilled for any r in the range $0 \le r \le 0.5$.
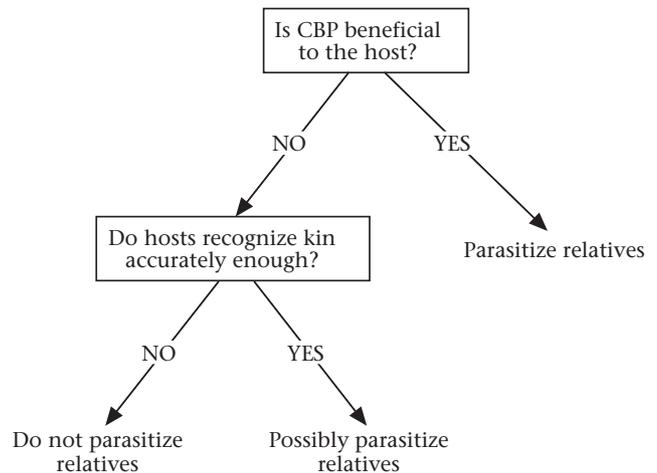

Figure 4. Schematic summary of our results. When egg dumping (CBP) is beneficial to the host, eggs should be laid preferentially in nests of relatives. However, if it is costly, preferential parasitism of relatives can evolve only when there is a sufficiently accurate kin recognition system and costs to the host are not too high.

precocial birds has been shown in some studies (e.g. Munro & Bédard 1977; Kehoe 1989). However, other studies have shown the opposite tendency (e.g. Andersson & Eriksson 1982) and each case should therefore be considered independently.

When parasitism is costly to the host's direct fitness, the extent to which kin recognition operates turns out to be crucial to determine whether parasitism should be

directed towards relatives or nonrelatives. To offset the cost of harming a relative, the parasite must experience a direct benefit from parasitizing a relative, if kinship is to promote conspecific brood parasitism. Such a direct benefit requires that related hosts are more likely to accept eggs from related parasites. This, in turn, requires that (1) relatedness is sufficiently high, otherwise it does not pay for hosts to accept any parasitic eggs, and (2) they are capable of recognizing kin eggs or laying parasitic females accurately enough.

Therefore, high relatedness between parasite and host, arising for example through female philopatry, can promote conspecific brood parasitism, but only if one of two conditions is met. Either parasitism should not be costly to the host (in which case it does not meet the definition of true parasitism) or, if it is costly, accepting kin eggs should nevertheless increase the inclusive fitness of the host (as in Andersson 2001) and the host must be equipped with a kin recognition mechanism that is sufficiently accurate. The higher the cost, the more accurate the recognition mechanism required. Our model also predicts that if parasitism is rarely detected in the first place, so that unrelated females often accept eggs, kin recognition is unlikely to improve acceptance probabilities sufficiently for kinship to promote CBP. Our findings agree with Andersson (2001) in that brood parasitism should be kin selected only if it is beneficial for both host and parasite in terms of their inclusive fitness.

Unfortunately, almost no study has measured host–parasite relatedness and costs of parasitism in the same population. Emlen & Wrege's (1986) study in white-fronted bee-eaters, *Merops bullockoides*, however, gives an interesting result that is consistent with our ideas. Chick survival in this altricial species is reduced with increased clutch size. Therefore, females predominantly parasitize nonrelatives. Furthermore, in the cases in which eggs are laid in the nest of a relative, 'parasitic' females provide help in chick rearing and so represent a benefit.

Opposite results regarding host–parasite relatedness have been reported in two recent studies on ducks (Anatidae). While Andersson & Åhlund (2000) found a nonrandom higher degree of relatedness between host and parasite in goldeneyes, *Bucephala clangula*, Semel & Sherman's (2001) study on wood ducks, *Aix sponsa*, showed avoidance of relatives as hosts. Studies considering costs and benefits of hosts and parasites give conflicting results in both of these species (goldeneyes: Andersson & Eriksson 1982; Eadie & Lumsden 1985; Milonoff et al. 1995; Eadie & Lyon 1998; wood ducks: Heusmann 1972; Clawson et al. 1979; Semel et al. 1988; Hepp et al. 1990), and it is likely that they vary between populations (Andersson & Eriksson 1982; Eadie & Lumsden 1985). Studies that combine measures of host–parasite relatedness and costs of parasitism at the same time are necessary to clarify their relation. Our model is simple enough for all the parameters to be measured relatively easily, which should allow quantitative tests of hypotheses on conspecific brood parasitism.

In moorhens, *Gallinula chloropus*, CBP is costly to the host (Gibbons 1986) and recognition of parasitic eggs seems to be absent (McRae 1995). Despite this, McRae &

Burke (1996) showed that the coefficient of relatedness *r* between hosts and parasites was high. In their study, however, host–parasite relatedness seems to be a by-product of female philopatry and hens do not seem to parasitize relatives preferentially (it is doubtful that they can recognize them). Our model assumes that parasites always have the choice of finding unrelated females' nests, and are therefore not constrained to use relatives as hosts. If philopatry is extremely strong and population density is low, this might not be the case, and our model does not then apply. The evolution of conspecific brood parasitism would follow different rules in such a case, and high relatedness might then favour acceptance of eggs without kin discrimination (generally, limited dispersal and the consequent 'viscosity' of the population can promote indiscriminate altruism towards neighbours, Mitteldorf & Wilson 2000). Whether philopatry can be so extreme in birds can be debated.

Our model is simple, in that it takes into account survival of offspring in the current brood only. Parasitized females may suffer additional costs not considered here, for example increased incubation effort (Thomson et al. 1998) may make parasitic eggs costly even if the host's own chicks subsequently survive better, or equally well, in larger broods. Our main argument, that parasites should avoid inflicting costs on relatives unless this brings about a direct fitness benefit to themselves, should remain valid when considering such additional costs. Another simplification we make is not including the possibility that parasites nest solitarily after being rejected. This possibility has been already considered in Andersson's (2001) model. We have tried to make our model simple to focus mainly on the effect of imperfect kin recognition on the evolution of CBP and make interpretations easier.

We can think of two ways in which kin recognition could operate. The first is kin recognition of parasitic females followed either by chasing off approaching non-kin before they lay eggs or by ejecting eggs seen to be laid by nonkin. The second possibility is kin recognition of the eggs. Avoidance or acceptance of parasitism through kin recognition of parasites before they lay the eggs is the most likely mechanism of response in birds. While kin recognition of individuals has been shown in birds (e.g. Bateson 1982) no evidence of nonself kin recognition of eggs has been found in this taxon. The majority of experiments on kin recognition of eggs in birds deal only with differentiation between own and foster eggs (e.g. Victoria 1972; Bertram 1979; Moksnes 1992; Grendstad et al. 1999; Welbergen et al. 2001). To our knowledge, no experiment has tried to find recognition of genetically related foster eggs against nonrelated ones. However, in some studies on passerines, the degree of acceptance of conspecific foster eggs is greater the more similar they are to the host eggs (Victoria 1972; Moksnes 1992). If egg pattern is a heritable trait, it could, in principle, act as a kin recognition cue: heritable variation in eggshell patterning is known in great tits, *Parus major* (Gosler et al. 2000) and village weavers, *Ploceus cucullatus* (Collias 1993). Some studies have provided evidence of recognition of genetically related eggs in other taxa (Masters &

Forester 1995; Faraji et al. 2000). Clearly, studies are needed to find out whether kin recognition of parasitic eggs is possible in birds.

Whatever the mechanism of kin recognition, it will reflect a difference in the probabilities of success in laying parasitic eggs for related (A_r) and unrelated females (A_O). These probabilities are unlikely to be one and zero, respectively. Not only the mechanism of kin recognition but also detection of parasitism can be inaccurate. In some species hosts are often unable to discriminate between their own and foster eggs after they begin egg laying (e.g. Lanier 1982; McRae 1995). If parasitism is seldom detected, A_O will be high and, even if hosts show a clear preference for kin when they detect parasitism (i.e. A_r is high), the ratio A_r/A_O is likely to be too low for relatedness to enhance conspecific brood parasitism.

Lyon & Eadie (2000) suggested that different degrees of costs and benefits of parasitism to the host determine the importance of kin selection in CBP and Andersson (2001) provided the first theoretical background to this idea. Here, we have emphasized the importance of the accuracy of kin recognition systems to the final outcome. Experimental studies that test the ability of birds to recognize parasitism by kin will surely cast light on the question of whether relatedness favours conspecific brood parasitism.

Acknowledgments

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