

Original Article

Strategy selection under conspecific brood parasitism: an integrative modeling approach

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Conspecific brood parasitism (CBP), where females lay eggs in nests of conspecifics, is taxonomically widespread. Following recent calls to consider CBP in a more integrative manner, we explore breeding strategies related to CBP by using a model of competing strategies that incorporates variation in individual quality, relatedness, recognition of own versus parasite-laid eggs, as well as the costs of egg laying and postlaying care. Our model creates 5 main conclusions. First, variation in individual quality plays a central role in shaping breeding strategies. Second, kinship plays a central role in the evolution of CBP. Third, egg recognition ability may affect the prevalence of parasitism: If hosts recognize parasitic eggs, relatedness between host and parasite facilitates CBP. Fourth, the relative costs of egg laying and postlaying care play a so far underestimated role in determining the prevalence of parasitism. Fifth, natal philopatry may lead to a reduction in productivity. To sum up, our theoretical study combines factors known to affect both breeding in general and CBP in particular and shows that these factors can explain a large proportion of the variation in CBP strategies found in the wild and therefore facilitates the understanding of the mechanisms shaping these strategies. *Key words:* breeding strategy, conspecific brood parasitism, cost of breeding, egg recognition, individual quality, kinship. *[Behav Ecol 22:144–155 (2011)]*

Conspecific brood parasitism (CBP) is an alternative reproductive strategy found in several egg-laying animal groups, including fish, insects, amphibians, and birds (Field 1992; reviewed by, e.g., Brockmann 1993; Wisenden 1999; Yom-Tov 2001; Tallamy 2005). CBP is especially common and well studied among waterfowl (Yom-Tov 2001). It is an intriguing reproductive mode for several reasons. It forms a relatively rare example of female alternative reproductive tactics (Lyon and Eadie 2008), and it has attracted a much wider range of evolutionary explanations compared with interspecific nest parasitism. Interspecific nest parasitism clearly relies on deception, whereas explanations of CBP range from true parasitism to kin-selected cooperation (Semel and Sherman 2001; Lyon 2003a, 2007; Pöysä 2004; Waldeck et al. 2008). Additionally, CBP has been hypothesized to have interesting population dynamical consequences (Lyon and Eadie 2008; de Valpine and Eadie 2008).

Another intriguing feature of CBP is that the roles of “parasite” and “host” are flexible and can be played by the same individual. Any effort to understand CBP should therefore assess how individuals should allocate reproductive effort between their own and other’s nests. Particularly, if egg recognition is possible and the host can destroy foreign eggs, a parasitic female will put some (or all) of her eggs in a risky situation. Given that these females often have a nest of their own, questions on parasitism must address why a female should only care for some of the eggs that she has laid.

Quoting Lyon and Eadie (2008): “Ultimately, because nesting females have their own nests, the key question is, Why don’t they lay the parasitic eggs in their own nests?”

A crucial difference between a parasitically laid egg and an egg cared for by the mother is that the former option frees the mother of all postlaying costs such as incubation of that egg (Monaghan and Nager 1997; Visser and Lessells 2001) or, if relevant, feeding that offspring. Laying costs, however, apply to both types of eggs. The choice to lay in one’s own nest versus parasitically could therefore be a contrast between low-investment eggs that may fail (if the host defends against parasitic eggs) and high-investment eggs with better survival prospects. These prospects can, obviously, depend on the clutch size, creating prospects for interesting game-theoretic feedback. For example, a large clutch in one’s own nest may make incubation inefficient or costly, which might select for eggs to be laid elsewhere, but if every individual practices this, all nests may become large, and this may select for limiting the number of eggs a female is prepared to incubate.

Additionally, recent studies have indicated the presence of factors giving rise to further complexity, such as kin selection through kin-biased egg donation (Andersson 1984; Loeb et al. 2000; López-Sepulcre and Kokko 2002; Loeb 2003; Waldeck et al. 2008; Jaatinen, Jaari et al. 2009). Obviously, imposing costs on other individuals has inclusive fitness consequences if hosts and parasites are related. Empirical studies have repeatedly found elevated relatedness among hosts and parasites (Andersson and Åhlund 2000; Loeb 2003; Roy Nielsen et al. 2006; Andersson and Waldeck 2007; Waldeck et al. 2008). The wide presence of such relatedness patterns indicates a possibility of mutual benefits from CBP (Andersson and Åhlund 2000; Andersson and Waldeck 2007; Waldeck et al. 2008) through kin selection (Hamilton 1964).

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However, any benefit, kin-selected or not, of CBP to either the host or the parasite will be contingent on the prospects of egg recognition, the maximum number of eggs hosts will care for, and maternal quality variation. Reflecting the complexity of the question, the literature regarding CBP by now contains a host of hypotheses explaining this alternative breeding strategy (Eadie et al. 1988; Andersson and Åhlund 2000; Tallamy 2005; Pöysä and Pesonen 2007). These hypotheses have received varying amounts of theoretical attention, and the need for an integrative theoretical examination of the central factors maintaining and regulating CBP has been growing with the number of hypotheses presented. Recently, there have been several calls to integrate the diverse theoretical treatments of CBP to form a more holistic picture. de Valpine and Eadie (2008), in their review of 18 theoretical studies, showed that very few had considered variation in maternal quality even though CBP is typically argued to be a flexible reproductive tactic, where an individual's maternal ability determines whether parasitism pays. It has also been suggested that some high-quality individuals may be able to double their reproductive output by employing parasitism parallel to breeding in a nest of their own (Andersson and Åhlund 2000), and indeed, it is typically argued that parasites do not form a distinct class in the population ("lifelong parasites" sensu Lyon and Eadie 2008), but the rules are much more flexible.

Here, we seek to theoretically examine emerging CBP strategies by combining factors known to affect both breeding in general and CBP in particular in egg-laying animals. We focus on 2 factors pertaining specifically to CBP, namely 1) relatedness between host and parasite and 2) the ability to recognize own versus parasite-laid eggs, and an additional 2 factors that are known to be important for life-history decisions in general: 3) individual quality and 4) the relative costs of egg laying versus costs of postlaying care. By doing so, we aim to clarify the mechanisms dictating choices of individual tactics and further the understanding of the basis for variation in CBP tactics. Moreover, we consider 5) a type of nonlinearity not usually present in CBP models yet possibly of importance in nature: Some offspring produced may compete locally with each other (in waterfowl, this usually occurs within the philopatric female sex; Anderson et al. 1992), which may diminish fitness gains of producing same-sex siblings.

THE MODEL

As stated above, our aim is to search for emerging strategies depending on specific individual features pertaining to breeding in general and CBP in particular. Because the fate of eggs clearly depends on host as well as parasite behavior, we build a model based on game theory for strategy selection. We describe the breeding strategy of an individual within a system of CBP as a set of reaction norms. These define the manner by which eggs are allocated between individuals' own nests and the nests of other individuals and the total number of eggs an individual will incubate. A tactic can be defined as a behavior, as dictated by the broader strategy, for a given situation. In other words, tactics are specific rules derived from the reaction norms, which in turn are termed strategies. The words "strategy" and "tactic" used in this paper will henceforth refer to these definitions.

We consider each individual female to have a strategy consisting of 3 reaction norms. The first reaction norm $A(q)$ dictates the number of eggs laid in one's own nest as a function of an individual's quality q . The second, $B(q)$, determines the number of eggs laid in other nests and the third, $C(q)$, the maximum number of eggs that an individual will take care of in its own nest. For example, in birds, a low $C(q)$ might mean that the female tosses out eggs in excess

of the number she is prepared to incubate and raise to fledging. The relatedness to eggs tossed out depends on average kinship to parasites but also on whether egg recognition is possible (see below). Because much of the literature on CBP derives from studies of waterfowl, we use the term "incubation" for the postlaying care described by $C(q)$, but note that this avian term generalizes to all forms of vitally important postlaying care. Also note that if $C(q) = 0$ and $B(q) > 0$, then females of quality class q do not attempt to care for offspring at all but specialize in parasitism. Thus, our model includes the lifelong parasite option discussed by Lyon and Eadie (2008). We do not impose any constraints, such as $A(q) \leq C(q)$, even though they may appear intuitively advantageous (e.g., if $C(q)$ is zero, then it makes sense for $A(q)$ to equal zero because when young require care to survive, selection should not favor laying eggs in one's own nest that are then abandoned and not cared for). We instead let all strategies freely evolve to see which solutions emerge as winners over evolutionary time.

In our evolutionary setting, the fitness of an individual depends not only on the actions of the focal individual but also on the actions of other individuals in the population. To mention an obvious example, if other individuals never accept parasitic eggs, then it will not pay to parasitize, no matter how cheaply eggs can be laid. This complexity together with the multidimensionality of each strategy prevents a straightforward mathematical solution of the optimal strategy, which is why we derive fitness numerically, as explained below.

Population structure and individual quality

Our model only considers female reproductive decisions, although we later differentiate between male and female offspring as fitness gains through the latter may be diminished through philopatry and local competition (see below). The population is divided into a number of quality classes q_i (in our examples, we use 10), and each individual is assumed to perceive its own quality perfectly. We define "quality" broadly as the capability or potential to outperform individuals of lower quality with respect to survival and therefore lifetime fitness. Thus, if 2 individuals lay and incubate exactly the same number of eggs, the higher quality individual is more likely to survive to the next breeding season. If a strategy dictates individuals to lay or incubate excessive numbers of eggs in relation to individual quality, this may markedly reduce survival, and the fitness of that strategy will be correspondingly lower, making other strategies replace it over evolutionary time. Thereby, quality ought to dictate the total number of eggs laid and cared for. Our measure of quality can be interpreted in several different ways, as for example, bodily condition, dominance, possession of territories of varying quality, or some other feature leading to differences in survival and individual performance.

Individuals in our model cannot perceive the quality of other individuals. Thus, a parasitic female, in effect, chooses recipients randomly with respect to quality. For simplicity, in our examples, all quality classes (1 ... 10) are assumed to be equally common in the population. We model dyadic interactions between hosts and parasites, noting that both individuals can potentially act as host as well as parasite to each other simultaneously. However, asymmetric interactions can emerge too (e.g., that one individual acts as host and the other as "parasite") because the individuals may use strategies that differ from each other, and if that is not the case, they may differ in quality, which makes them utilize different tactics within the same strategy. The overall fitness associated with a strategy will then be calculated over all possible dyadic pairs.

Number of eggs and egg recognition

The first step is to calculate the number of eggs in each nests, when individual i of quality q_i using the strategy $\Phi_i = \{A_i(q_i), B_i(q_i), C_i(q_i)\}$ is playing against individual j of quality q_j using the strategy $\Phi_j = \{A_j(q_j), B_j(q_j), C_j(q_j)\}$. Note that this does not exclude cases where the 2 individuals are of identical quality and/or using identical strategies. The total number of eggs, E_i , in the nests of these individuals is given by

$$E_i(\Phi_i, \Phi_j, q_i, q_j) = \min \{ [A_i(q_i) + B_j(q_j)], C_i(q_i) \}. \quad (1)$$

Individual j 's nest, E_j , can be derived symmetrically by exchanging subscripts i and j . This formulation specifies the rule that if the total number of eggs laid in a nest, $A_i + B_j$, exceeds the threshold C_i , the surplus is discarded (not cared for).

Equation 1 only dictates the total number of eggs in a nest. The composition of the clutch, that is, the proportion of non-parasitic and parasitic eggs, must be calculated separately. Egg recognition, by which we mean any process that leads to information about the identity of parasitic eggs, facilitates host control over the composition of the clutch in its nest. With perfect egg recognition, an individual is able to selectively discard parasitic eggs from its nest (if it pays for it to do so). In the absence of egg recognition, eggs can only be discarded randomly. Note that our definition of "egg recognition" includes any processes that aid assessing the identity of eggs within a clutch. For example, the direct observation of a parasitic individual depositing a parasitic egg falls within this definition, although the egg itself may not be recognizable. We first consider 2 extremes. With perfect recognition, a female can choose to prioritize its own eggs or to incubate parasitic eggs if that proves beneficial. In the absence of recognition, a female who cannot incubate all the eggs laid in its nest has no choice but to exclude eggs randomly from incubation, which in turn will lead to a fraction of its own eggs being excluded as well.

With perfect egg recognition, the proportion P_{ii} of eggs in nest i that are laid by individual i (i.e., the individual's own eggs in its own nest) is given by

$$P_{ii}(\Phi_i, \Phi_j, q_i, q_j) = \min \left\{ 1, \frac{A_i(q_i)}{E_i(q_i)} \right\} \quad \text{if } E_i(q_i) > 0, \quad (2a)$$

$$P_{ii} = 1 \quad \text{if } E_i(q_i) = 0.$$

In the absence of egg recognition, this proportion becomes

$$P_{ii}(\Phi_i, \Phi_j, q_i, q_j) = \frac{A_i(q_i)}{A_i(q_i) + B_j(q_j)} \quad \text{if } A_i(q_i) + B_j(q_j) > 0, \quad (2b)$$

$$P_{ii} = 1 \quad \text{if } A_i(q_i) + B_j(q_j) = 0.$$

As with Equation 1, the corresponding proportion P_{jj} for individual j can be derived symmetrically by exchanging subscripts i and j . Note that when the total number of eggs in the nest is 0, we have, for the sake of mathematical convenience, defined the proportion i eggs to be 1. This will naturally be multiplied by the number of eggs to yield the correct product 0.

Our model easily extends to partial recognition (between 0 and 1), achieved by making P_{ii} and P_{jj} a weighted average of Equations 2a and 2b. However, due to the large number of variables and possible combinations, we only present the extreme cases of absence of recognition and perfect recognition in this study.

Exclusion of eggs refers to any behavior through which eggs end up not being taken care of, be they rejected, buried, or subject any other lethal and incubation effort-saving behavior. If a parasite is not allowed to lay in the hosts nest, the model assumes the parasitic eggs, intended to be laid in the hosts nest, to be wasted, thus creating negative selection pressure on the parasitic tactic.

Fitness gains per reproductive bout

The fitness gains per reproductive bout of individual i of quality q_i who is parasitizing and being parasitized by individual j of quality q_j can now be defined as

$$W(\Phi_i, \Phi_j, q_i, q_j) = E_i P_{ii} + r E_i (1 - P_{ii}) + E_j (1 - P_{jj}) + r E_j P_{jj}. \quad (3)$$

Here r is the average relatedness between host and parasite in the population. The relatedness values play a role in strategy selection by accruing inclusive fitness gains for hosts and parasites receiving eggs from relatives and donating eggs to relatives, respectively. The use of average relatedness is a simplification of reality, and it should be noted for potential future refinement that exceptionally long-lived individuals may have more relatives in the population with which they may interact, which increases their relatedness to the rest of the population above the average. Note that our formulation assumes equal survival of all offspring that receive postlaying care in a nest, regardless of clutch size or maternal quality. This assumption can be relaxed in future models to include, for example, predator dilution effects (Boland 2003; Whitfield 2003).

Survival, laying costs, and postlaying costs

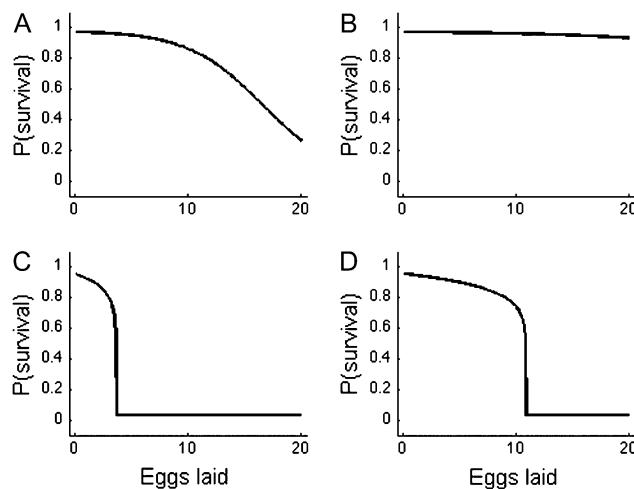
Lifetime reproductive success will be based on Equation 3, but it is also affected by costs, which determine the probability that an individual survives through one reproductive bout, and thus the individual's expected longevity. These are assumed to depend on the quality of the individual as well as egg-laying costs and postlaying costs.

We denote laying and postlaying (incubation) costs by α and β , respectively. The cost of laying is always inflicted on the individual producing eggs, independently of where the egg is laid. Our assumption that parasitic laying is as costly as laying in one's own nest can be considered a simplification of reality, where parasitic laying may per se inflict, for example, travel costs, or costs related to leaving the own nest exposed to predation or parasitism by other females, yet for the sake of clarity, we do not consider these costs here (see DISCUSSION). The total incubation cost is a function of eggs incubated, whether these are parasitic or nonparasitic.

We assume that both laying costs α and postlaying costs β impact survival negatively. However, our assumption that the population consists of individuals differing in quality implies that some individuals can bear the costs better than others. Thus, the survival function S should be an increasing function of individual quality q and a decreasing function of the total laying and postlaying costs (which depend on α , β , and the number of eggs laid and cared for, respectively). Our examples are based on the function

$$S(A(q), B(q), C(q), q) = \varphi \frac{1}{1 + e^{-\lambda}}. \quad (4.1)$$

Here φ ($0 < \varphi < 1$) is an upper bound for the annual survival probability, and

**Figure 1**

Examples of shapes of 2 different survival functions: Equations 4.1 and 5. (A) and (B) represent the survival function described in Equation 4.1 and (C) and (D) that described by Equation 5. (A) and (C) show the probability of survival for an individual of medium quality ($q = 5$), depending on the number of eggs laid, where all eggs are laid in the own nest. (B) and (D) show the same probability for medium-quality individuals who lay all their eggs parasitically. Other parameter values: $r = 0$, $\alpha = 0.1$, $\beta = 0.2$, $\phi = 0.98$.

$$\lambda = q_i - \alpha [A(q_i) + B(q_i)] - \beta E_i(q_i). \quad (4.2)$$

In order to assess the robustness of our model, we also implemented an alternative survival function of a very different shape

$$S(A(q), B(q), C(q), q) = \sqrt[10]{\min\{1, \gamma\}} \quad \text{if } \gamma > 0, \quad (5)$$

$$S(A(q), B(q), C(q), q) = 0 \quad \text{if } \gamma \leq 0,$$

$$\text{where } \gamma = 0.4 + 0.5 \frac{q_i}{q_{\max}} - [\alpha(A(q_i) + B(q_i)) + \beta E_i(q_i)] \left[1.1 - \frac{q_i}{q_{\max}} \right],$$

where q_{\max} is the highest (10th) quality class; this choice produced qualitatively similar results to that of the chosen main function (Equation 4.1). The different shapes of the 2 survival functions are illustrated in Figure 1. Henceforth, we will only show the results of our main function unless otherwise stated.

The survival function is used to calculate the probability that an individual survives to the end of a single reproductive bout and the subsequent nonbreeding season, taking into account the individuals expenditure of resources on various tasks related to reproduction (here: egg laying and incubation) as well as individual quality. This survival probability is then used to calculate expected life spans (Equation 6), which are finally used to calculate the total lifetime fitness (Equation 7):

$$L = \sum_{k=0}^{\infty} k S^k (1 - S) = \frac{S}{1 - S}, \quad (6)$$

where k is the number of reproductive bouts, and

$$W_{\text{tot}} = W \times L. \quad (7)$$

Simulation

Each simulation was run for a large number of generations N . Preliminary trials of convergence were performed using values of N between 200 000 and 20 000 000, and the model was found to converge well before $N = 10 000 000$; thus, subsequent simulations were performed using $N = 10 000 000$. The initial resident strategy was created by randomly assigning tactics $A(q)$, $B(q)$, and $C(q)$ independently to all condition classes q_i . To reflect biologically meaningful clutch sizes, values for these tactics (egg numbers) were drawn from a uniform distribution between 0 and 20 (integers only). Each “generation,” we created a random mutant using the same distributions that created the initial resident strategy. The fitness of the mutant strategy was then calculated (Equations 1–7) as a mean of all possible dyadic combinations ($i = 1 \dots 10$ and $j = 1 \dots 10$), where the mutant is of quality q_j and the resident individual is of quality q_i . This was compared against the fitness of the resident strategy derived in a population of residents.

When the fitness of the new strategy was higher than that of the resident strategy, the new strategy was assumed to invade the population and replace the resident strategy before the cycle started again. For the next round, the invasive strategy replaced the resident strategy. For each set of parameters, this simulation was replicated 20 times to check for convergence from diverse starting conditions (randomly chosen ancestral strategies). The final strategy for each replicate was saved. We also recorded the lifetime fitness of each quality class to check for consistency of the model: Fitness should increase along with individual quality; otherwise, some quality classes are still performing suboptimally. Our choice of $N = 10 000 000$ led to consistent patterns where fitness increased with individual quality.

Limit of postlaying care and realized postlaying care

The term $C(q)$ refers to the maximum total number of eggs an individual of given quality will care for. In many cases, the total number of eggs in a nest was smaller than the mother's $C(q)$. In these cases, it is important to distinguish between $C(q)$ and the average number of eggs that actually receive care. The average number of eggs cared for by an individual of quality q_i is given by calculating the average of E_i (Equation 1) over all the opponents' quality classes q_j . This is only calculated at the end of the simulation run, where we assume that all individuals of quality q now use the same optimal strategy $\Phi = \{A(q), B(q), C(q)\}$:

$$\bar{E}_i = \frac{\sum_{j=1}^{j_{\max}} E_i(\Phi, \Phi, q_i, q_j)}{j_{\max}} = \frac{\sum_{j=1}^{j_{\max}} \min\{[A(q_i) + B(q_j)], C(q_i)\}}{j_{\max}}. \quad (8)$$

Natal philopatry

Waterfowl are an important taxonomic group in which CBP is common and well studied (Yom-Tov 2001). These birds also often exhibit sex-biased natal philopatry: Female offspring return to their natal area and male offspring mainly disperse elsewhere (Anderson et al. 1992). Although natal philopatry may result in proximity to relatives and thereby facilitate cooperative behavior, it may also reinforce competition for local resources among relatives (Franks 1998). This can clearly alter the fitness gain functions of reproduction, whether or not eggs are parasitically laid, as it diminishes the profitability of large broods: Extra offspring yield little parental fitness if

these are female who will compete with one another, their mother, and their future offspring for resources. The severity of this local competition increases with the number of females produced, whereas the fitness gains from male offspring may have a more linear nature. Previous models regarding CBP have overlooked female natal philopatry as a component affecting the strategy outcomes of brood parasitic animals. In an extension of our model, we apply a diminishing returns function to the fitness gains received from producing females to account for local competition.

In the basic model, offspring of both sexes were treated equally. To account for female-biased natal philopatry, we must consider male and female offspring separately. It is assumed that the offspring sex ratio is fixed at 1:1, so the total number of female eggs in a given individual's nest is $E_i/2$. The same applies to male eggs. Because females are likely to breed at or near their place of origin and compete with each other, an increasing number of female eggs in a nest will lead to diminishing fitness returns. To account for this, we use the "effective number of female eggs":

$$F_i(\Phi_i, \Phi_j, q_i, q_j) = \frac{\left(10 \frac{E_i}{2}\right)}{\left(9 + \frac{E_i}{2}\right)}. \quad (9)$$

This function has the desired properties: When the number of eggs is small, the fitness returns are diminished very little or not at all. As the number of eggs increases, the fitness returns from female eggs show diminishing returns toward an upper limit (10 in this case).

However, if the average fitness gains per female offspring are reduced, the same must happen to the average fitness gains per male offspring. This is due to the Fisher condition (see Houston and McNamara 2005; Kokko and Jennions 2008), which states that male and female reproductive success are logically intertwined because each offspring has precisely one genetic father and one genetic mother. Thus, parents should not be assumed to gain systematically more fitness through sons than through daughters, which would easily (and erroneously) happen if the fitness gains were varied independently. Therefore, even though the fitness returns per male offspring remain linear, they must be corrected by a "Fisher factor":

$$\eta = \frac{\sum_{i=1}^{i_{\max}} \left(\sum_{j=1}^{j_{\max}} F_i(\Phi_i, \Phi_j, q_i, q_j) \right)}{\sum_{i=1}^{i_{\max}} \left(\sum_{j=1}^{j_{\max}} \frac{E_i(\Phi_i, \Phi_j, q_i, q_j)}{2} \right)}. \quad (10)$$

Now, we can calculate the effective number of eggs in the nest of individual i :

$$\hat{E}_i(\Phi_i, \Phi_j, q_i, q_j) = F_i(\Phi_i, \Phi_j, q_i, q_j) + \eta \frac{E_i(\Phi_i, \Phi_j, q_i, q_j)}{2}. \quad (11)$$

To account for local female competition, the simulations were run as before but with E_i and \hat{E}_i in Equation 3 replaced by \hat{E}_i and \hat{E}_j . All other equations remain the same as in the basic model.

RESULTS

After initially very rapid changes in the resident strategy, replacements of residents by mutants occurred with decreasing frequency. The fitness of individuals became a steadily growing function of individual quality, indicating in its part that the model is performing in the intended manner.

(a) Individual quality

Tactics of individuals depended strongly on individual quality. In the absence of egg recognition, this produced a dichotomy between pure parasites and nesting parasites (Figure 2A-C; Table 1), a life-history feature suggested by Lyon (1993a) as well as by Åhlund and Andersson (2001), though in a lifetime sense, this has been argued to be rare (Lyon and Eadie 2008). Our results show, however, lifelong specialization to be at least a theoretical possibility. Dichotomous specialization in purely parasitic females and nesting parasites likewise emerged as a possibility when implementing the alternative survival function (Equation 5), although this survival function produced a slightly more pronounced transition from pure to nesting parasitism (NP). The existence of similar solutions in 2 very different survival scenarios confirms the theoretical possibility of such a dichotomy.

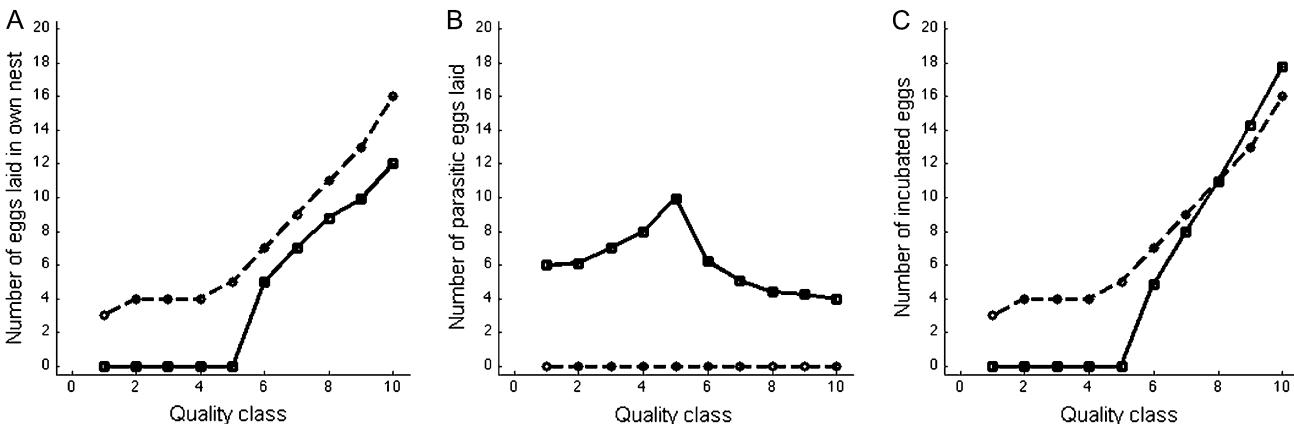


Figure 2

(A) The effect of individual quality and egg recognition on the number of eggs allocated to the own nest ($A(q)$), (B) parasitically laid eggs ($B(q)$), and (C) the total number of eggs incubated ($C(q)$). The figures are based on absence of recognition (solid line with square markers) and perfect recognition (dashed line with circle markers). In the absence of recognition, a clear quality determined dichotomy emerges between pure parasites and nesting parasites, and the parasitic tactics flourish. With perfect recognition, no hosts accepted any parasitic eggs owing to the lack of inclusive fitness benefits. Other parameter values: relatedness $r = 0$, $\alpha = 0.1$, $\beta = 0.2$, $\phi = 0.98$.

Table 1
Summary of strategy outcomes based on Figure 6

	High egg-laying cost	High postlaying cost
Low quality ($q < 0.5$)	Parasitize	Parasitize (increased)
High quality ($q \geq 0.5$)	Mixed (increase eggs in own)	Mixed (increase parasite eggs)

In most cases, our model produced a pattern very common in nature: that individuals may simultaneously (i.e., in the same breeding season) function as hosts as well as parasites. The only cases where no quality classes acted as parasites and hosts simultaneously were those where the parasitic tactic was not viable, that is, in the absence of relatedness ($r = 0$) when egg recognition was perfect (thus, parasite eggs were never accepted). The relative proportion of parasitically laid eggs was often strongly quality dependent, with the proportion of parasitically laid eggs declining with increasing quality (e.g., Figure 3A,B). The only exceptions were pure parasites of increasing quality. These females, by definition, did not show any change in this proportion (Figure 1A,B; quality classes (q) 1 ... 5) because all their eggs were parasitically laid.

(b) Relatedness

Host relatedness to parasites clearly impacted the evolution of brood parasitism. In the presence of egg recognition, the role of relatedness was at its strongest: It completely determines the presence or absence of parasitic tactics (Figure 3B; Table 2). With perfect recognition, the parasitic strategy was not viable at all in the absence of relatedness and costly postlaying care. Hosts in this case have full control, and no host could benefit from accepting parasitic eggs. On the other hand, positive relatedness leads to benefits for hosts and thereby to acceptance of eggs, which then favors parasitism. The total number of eggs given postlaying care by hosts was insensitive to relatedness to parasites (Figure 3C). Instead, the number of eggs laid into own nests was reduced with elevated relatedness (Figure 3A), showing the theoretical presence of benefits from clutch reduction, a finding supporting empirical and theoretical results regarding clutch reduction under CBP

(Andersson and Eriksson 1982; Erikstad and Bustnes 1994; Lyon 1998; Jaatinen, Jaari et al. 2009). The number of eggs laid in the own nest decreased, whereas the number of eggs laid parasitically did not increase to fully compensate for the decrease in the own nest, with the exception of quality class 9. Thus, there is a redistribution of eggs as well as a reduction in the total number of eggs (Figure 3A,B). Indeed, in the presence of relatedness and recognition, hosts reached higher fitness levels by reducing their clutch and receiving indirect fitness benefits from the eggs of relatives being laid in to their nests. The increased fitness was reached through a longer life-span that individuals could reach by allocating their resources in this manner.

(c) Recognition of own versus parasite-laid eggs

The presence or absence of egg recognition had a central role in dictating the nature of parasitism because it altered the control that hosts have over eggs they care for. In the presence of perfect recognition, the outcome was strongly dependent on relatedness as mentioned above. Perfect recognition in the absence of any relatedness between the host and the parasite yielded no postlaying care for any parasitically laid eggs (Figure 4). This renders the parasitic tactic unviable and thus absent (Figure 2B; Table 3). Positive relatedness led to a situation where individuals accepted the eggs of parasites, and thus, the parasitic tactic was viable (Figure 3B; Table 2).

In the absence of recognition, on the other hand, we observed an interesting dichotomy between purely parasitic tactics, and tactics were both nesting and parasitism where present (Figure 1A–C). Low-quality individuals that cannot easily afford a nest of their own have, in the absence of recognition, ample opportunities to lay parasitic eggs. With increasing quality, however, a threshold was reached where nesting became more beneficial to them than parasitism. As a consequence, the number of parasitic eggs decreased, with effort reallocated to laying eggs in one's own nest at this threshold (Figure 1A,B).

(d) The cost of egg laying and postlaying care

The results given in (c) assume low postlaying costs of care. The relative costs of egg laying and postlaying care can vary between systems, and this turns out to have an impact on the feasibility of cooperative strategies among kin (in this case,

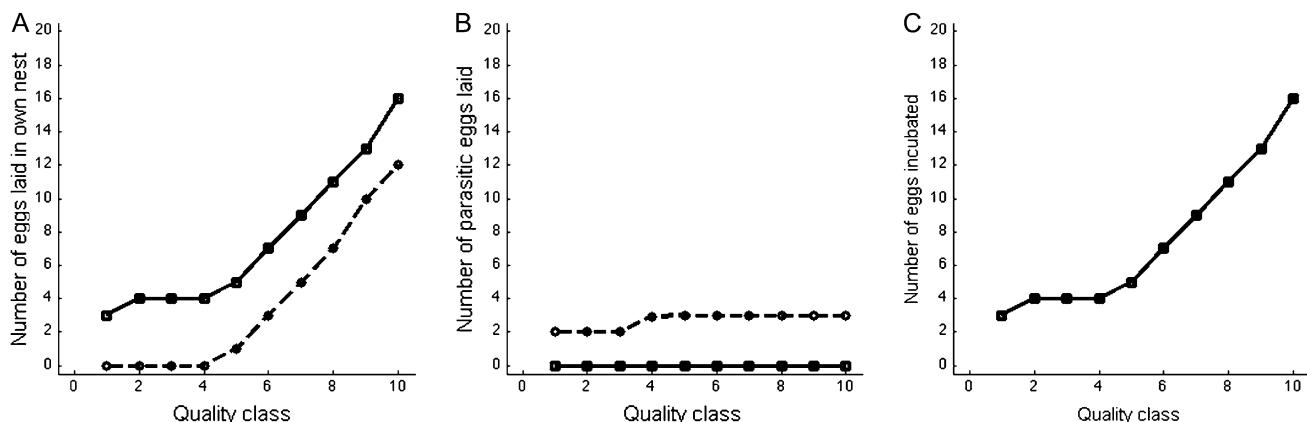


Figure 3

(A) The effect of relatedness on the number of eggs allocated to an individual's own nest ($A(q)$), (B) parasitically laid eggs ($B(q)$), and (C) the total number of eggs incubated ($C(q)$). The figures are based on relatedness values of 0 (solid line with square markers) and 0.5 (dashed line with circle markers). Positive relatedness leads to a reduction in host clutch size and the evolution of parasitism, whereas the total number of incubated eggs is unaffected by relatedness to parasites. Other parameter values: perfect egg recognition, $\alpha = 0.2$, $\beta = 0.1$, $\phi = 0.98$.

Table 2
Summary of strategy outcomes based on Figure 3

	$r = 0$	$r = 0.5$
Low quality ($q < 0.5$)	Nest	Parasitize
High quality ($q = 0.5$)	Nest	Mixed

the acceptance of parasitically laid eggs). A high postlaying cost can override hosts' potential inclusive fitness benefits of receiving eggs from relatives. Hosts able to recognize eggs are then expected to prefer their own eggs above their relatives' eggs, which in turn hinders the deposition of foreign eggs (Figure 5).

In the absence of egg recognition, the relative cost of egg laying and postlaying care had a clear effect on the allocation of eggs between nests. Generally, when postlaying care was more expensive than laying, the number of eggs laid in the own nest was lower and more eggs were laid parasitically (Figure 6A,B). Individuals of low and medium quality were particularly sensitive to care costs, evolving to provide care for a much larger number of eggs when postlaying care was less costly (Figure 6C). With increasing quality, this sensitivity diminished, and quality itself, rather than the relative cost of laying versus post-laying care, determined the size of accepted clutches (Figure 6C). When the egg-laying cost was high relative to postlaying costs, individuals laid more eggs into their own nests (Figure 6A) and less eggs parasitically (Figure 6B). In the presence of relatedness, high egg-laying costs also lead to care provisioning (e.g., incubation) being beneficial from lower condition classes onward, sometimes even before sufficient levels of quality for laying own eggs had been reached (Figure 6A,C). This predicts an intriguing strategy where individuals, not being able to afford to lay eggs, give postlaying care to eggs of relatives and thereby accrue some—albeit small—inclusive fitness benefits.

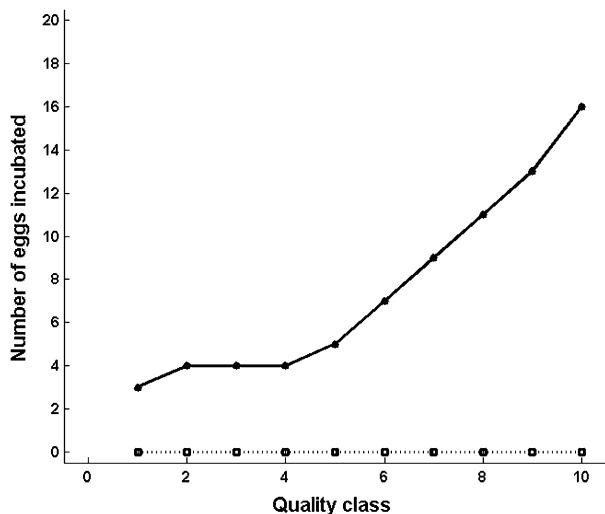


Figure 4

The number of eggs incubated assuming perfect egg recognition and no relatedness ($r = 0$). No parasitic eggs are accepted (dotted line and square markers). In this figure, the number of own eggs given postlaying care (solid line and triangle markers) and the total number of eggs (dashed line and circle markers) given postlaying care are identical. Thus, lacking inclusive fitness benefits, hosts who have full control over the composition of their clutch do not accept parasitic eggs. Other parameter values: $\alpha = 0.1$, $\beta = 0.2$, $\varphi = 0.98$.

Table 3
Summary of strategy outcomes based on Figure 2

	No recognition	Perfect recognition
Low quality ($q < 0.5$)	Parasitize	Nest
High quality ($q = 0.5$)	Mixed	Nest

(e) Natal philopatry

The presence of natal philopatry and the associated increase in local competition did not significantly change the strategy outcomes. However, with natal philopatry present, we observed a slight overall trend to decrease egg production. Regardless of this slight reduction, the effects of the other 4 components of CBP (sections a–d above) remained unchanged.

DISCUSSION

An important insight emerging from our study is that it is not a priori clear how individuals should allocate reproductive effort between their own and other's nests (Takasu 2004). Our results particularly highlight the central role of individual quality in shaping the sets of reaction norms inherent in CBP strategies. Likewise, the interplay between relatedness and egg recognition was found to affect the nature of CBP strategies. A low or moderate cost of parental care has been suggested to be the reason why CBP occurs so frequently in precocial species (Rohwer and Freeman 1989; Arnold and Owens 2002). The patterns of presence and absence of parasitic tactics produced by our model agree with these suggestions. Depending on the reigning social and ecological circumstances, the strategies range from purely parasitic to more cooperative tactics and from high prevalence of CBP

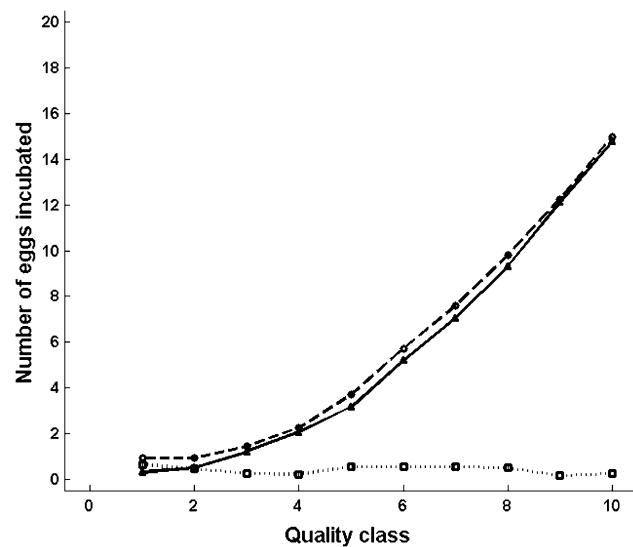


Figure 5

The number of eggs incubated assuming perfect egg recognition and relatedness ($r = 0.5$). Despite positive relatedness and full recognition, virtually no parasitic eggs are accepted (dotted line and square markers), and the number of own eggs provided with post-laying care (solid line and triangle markers) very closely matches the total number of all eggs cared for (dashed line and circle markers). In this scenario, the high cost of postlaying care ($\beta = 0.2$) outweighs the potential inclusive fitness benefits provided by host-parasite relatedness, and hosts consequently discriminate against parasitically laid eggs. Other parameter values: $\alpha = 0.1$, $\varphi = 0.98$.

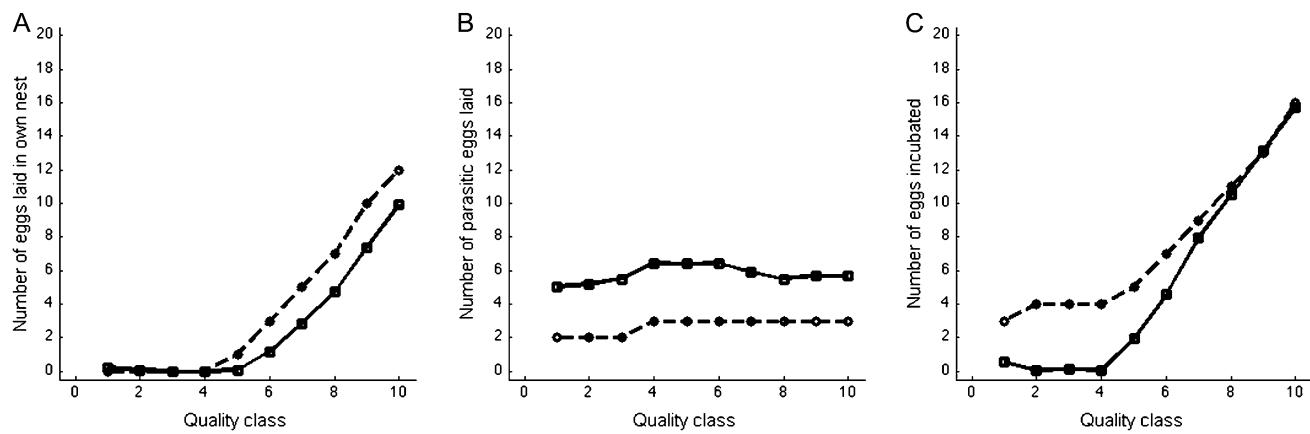


Figure 6

(A) The effect of egg laying and postlaying care costs on the number of eggs allocated to an individual's own nest ($A(q)$), (B) parasitically laid eggs ($B(q)$), and (C) the total number of eggs incubated ($C(q)$). The solid line with square markers represents a situation where postlaying care is the higher cost ($\beta = 0.2$). This scenario shows fewer eggs laid into the own nest and provided with postlaying care and an elevated number of eggs laid parasitically. The dashed line with circle markers represents the opposite a situation where egg laying is the higher cost ($\alpha = 0.2$). This increases the number of eggs laid into one's own nest and decreases the number of parasitically laid eggs. Other parameter values: relatedness $r = 0.5$, egg recognition absent, $\phi = 0.98$.

to the total absence of parasitism. These results (summarized in Table 4) corroborate the findings of both Andersson (2001) and López-Sepulcre and Kokko (2002). Additionally, the relative balance of egg-laying and postlaying (care) costs was found to regulate the net outcome of cooperative behavior. In some cases, postlaying costs could override the benefits of potential cooperation and prevent cooperative forms of CBP from evolving. In the following, we will consider each of the 5 investigated factor in turn.

Individual quality

It has been suggested that individual quality affects strategy selection (Sorenson 1991; Lyon and Eadie 2008) and that superior individuals outperform inferior individuals in terms of reproductive output (Åhlund and Andersson 2001; Kim and Monaghan 2005; Hamel et al. 2009). Our results are in line with these arguments: Individual quality has a profound effect on the selection of tactics and thereby a central role in shaping CBP strategies. In addition, individual variations in strategy selection have been proposed to cause dramatic fitness differences (Lyon 1993a; Åhlund and Andersson 2001). Our model

not only supports this notion but also suggests that a single strategy, which includes condition dependence (a reaction norm), may explain several empirically documented CBP tactics. For example, individual quality differences have been suggested to lead to diverging modes of reproduction (Lyon 1993a; Åhlund and Andersson 2001; Lyon and Eadie 2008). By visualizing the results of Sorenson (1991), Lyon and Eadie (2008) show the effects of a gradient in phenotypic and ecological constraints: Individuals move from nonnesting through parasitism to nesting, and finally, when conditions for breeding are at their best (i.e., lowest constraints), individuals are able to combine parasitism with nesting. This combination of tactics, also termed NP, is regarded as a costly yet productive way to increase fitness (Åhlund and Andersson 2001).

Our results clearly show that quality differences may translate into great fitness differences, as suggested by empirical work (Åhlund and Andersson 2001). Contrasting with both Åhlund and Andersson (2001) and Sorenson (1991), however, the intermediate tactic of nesting without parasitizing did not emerge. The parasitic tactic seemed to switch straight into a NP tactic as quality increased. This may be a side product of the relatively extreme values of relatedness and egg recognition that we used, or the lack of an intermediate nesting strategy may also be the result of a cost of parasitism, which has not so far been modeled. Also note that our model assumed that laying costs were the same for parasitic and non-parasitic eggs; it remains to be seen if including higher costs for parasitically laid eggs would make nesting without parasitism stable.

Individual variation in quality is common in nature, yet its central role in shaping CBP strategies has only once previously been acknowledged in theoretical work (Maruyama and Seno 1999). This previous study does not, however, view the different tactics as products of individuals employing different tactics within a broader strategy depending on their quality. Maruyama and Seno (1999) instead view parasites as pure parasites and hosts as superior quality individuals who do not engage in parasitism. In our view, the incorporation of quality variation, and the associated variations in tactics within broader strategies, not only provides a further degree of realism but also provides a theoretical foundation for empirical studies (Lyon 1993a; Åhlund and Andersson 2001). Our model reveals the possibility that a single strategy may dictate

Table 4

Summary of the nature of parasitism depending on egg recognition, relatedness and the costs of egg laying (α), and postlaying care (β)

	Egg recognition absent		Egg recognition present	
	$\alpha > \beta$	$\alpha < \beta$	$\alpha > \beta$	$\alpha < \beta$
Relatedness = 0	—	—	0	0
Relatedness = 0.5	+	—	+	0

Minus signs (—) represent true parasitism and conflicting interests of host and parasite, whereas plus signs (+) represent cooperative behavior benefiting both host and parasite. Zeros (0) represent situations where no parasitism occurs as a result of egg recognizing hosts rejecting parasitism due to a negative balance between costs and benefits of parasitism. This table summarizes the main results of our integrative CBP model and shows that high host-parasite relatedness may accrue benefits for hosts regardless of egg recognition but only when post-laying care is relatively cheap.

a whole range of tactics and thereby provides a potential solution to the disparities between several seemingly different explanations for the presence of CBP in populations.

Relatedness and egg recognition: Does CBP reflects conflict or cooperation?

The central consequence of positive relatedness between host and parasites is the prospect of inclusive fitness benefits (Hamilton 1964; Andersson 1984, 2001; López-Sepulcre and Kokko 2002). These may reduce the cost of CBP or even completely outweigh the costs of receiving foreign eggs (Andersson and Eriksson 1982; Lyon and Eadie 2000; Andersson 2001; López-Sepulcre and Kokko 2002; Roy Nielsen et al. 2006), thus rendering the term “parasitism” somewhat inappropriate in this context. The effects of relatedness on strategy outcomes have thus to be viewed together with the costs of receiving the eggs. The process of receiving eggs is, in turn, dependent on the control over parasite behavior exhibited by hosts, termed “egg recognition” in this study. To sum up, the balance between inclusive fitness benefits and the costs of receiving eggs determines the willingness of hosts to receive eggs, whereas host control over parasite behavior determines the capability of hosts to either to accept or to reject eggs. We found that in the absence of egg recognition, the role of relatedness became less pronounced, and it mainly influenced solutions by creating indirect benefits for the purely parasitic tactic. In the presence of recognition, on the other hand, the degree of relatedness plays a truly important role in shaping CBP strategies (see also López-Sepulcre and Kokko 2002).

We found indications of a dichotomy between cooperation and conflict regulated by the interplay between relatedness and egg recognition. Given sufficiently high relatedness between host and parasite and sufficiently low cost of postlaying care, eggs were always accepted regardless of egg recognition. Cooperation can thus emerge without kin recognition if locally interacting individuals are sufficiently related (note that in a wider context, this requires that the offspring of each female do not compete locally too strongly, e.g., West et al. 2002; Mouden and Gardner 2008; however in our study, local competition had a relatively minor effect).

In the absence of relatedness, hosts that were able to distinguish between own and foreign eggs did not accept eggs of the latter type, rendering parasitism an unviable tactic (Figures 3A–C and 4; Table 2). Contrastingly, when hosts were unable to detect parasitic eggs, and so lacking control over the deposition of eggs into their clutches, parasitic tactics (in the true sense) were found to flourish (Figure 2A–C; Table 3). That under such circumstances half of the quality classes employed the parasitic tactic alone (Figure 2A,C; Table 3) indicates that the benefits of nesting outweighed those of parasitizing only for relatively high-quality levels (Figure 2A). The initiation of own nesting from a certain condition class onward was followed by a decrease in the number of eggs laid parasitically (Figure 2A,B). The presence of non-nesting parasites has been documented in several CBP studies (e.g., Lyon 1993a; Forslund and Larsson 1995). Our results suggest that the degree of host–parasite relatedness and egg recognition is likely to regulate the success of such “floaters.” Furthermore, if parasites are shunted from one nest, they may be successful at another, which may reduce negative selection against parasitism and help to make it a viable strategy. Hosts may differ in their ability to reject parasites, and this can be modeled using egg recognition values intermediate to the ones used in this study.

A clear dichotomy of “cooperative” and “conflicting” interactions between host and parasite has not been documented in

any one species. However, comparing features of CBP between species reveals varying emphasis on cooperation versus conflict. In the common goldeneye (*Bucephala clangula*), parasites have been found to be related to the host, laying more eggs in a related host’s nest than expected by random laying (Andersson and Åhlund 2000). It has been suggested that the mechanism leading to such kin-biased egg donation is the result of birth nest mates recognizing and targeting one another when laying parasitically (Andersson and Åhlund 2000). In addition, lace bug (*Gargaphia solani*) females have been found to accrue inclusive fitness by preferring to oviposit into the clutches of relatives, often half sisters ($r = 0.25$) and full sisters or parent–offspring pairs ($r = 0.5$) (Loeb 2003), a preference that may be driven by genetically determined olfactory cues (Loeb et al. 2000).

Contrastingly, American coots (*Fulica americana*) have not been found to exhibit nonrandom egg donation (Lyon 1993b). Strong constraints on brood size, imposed by expensive brood care, offer a possible explanation. Parasitism is very costly for the host in this species, and hosts have evolved sophisticated means by which they recognize parasitic eggs and mitigate their negative impact on the survival of the natal young (Lyon 2003b, 2007). The behavior of these hosts markedly reduces the fitness of the parasitic tactic (Lyon 1993b), lending empirical support to the prediction that perfect recognition renders parasitism nonprofitable, although we did not explicitly consider the evolutionary trajectory toward better recognition ability. As stated by Lyon (2007), defensive capabilities of hosts may be age dependent: Younger coots may reject eggs less often than older ones, reflecting age- or experience (quality)-dependent variation in egg recognition capabilities. It should be noted, however, that for simplicity, our model concentrates on costs paid by the parent and only includes very simple effects of CBP on offspring (which come in 2 forms: rejected eggs die, and female offspring may suffer from local competition). In nature, it is possible to find more diverse relationships including the possibility that offspring experience positive effects (e.g., due to predation dilution), whereas the negative effects on the parent can be substantial, for evidence on avian incubation costs, see Thomson et al. (1998). Although more extensive modeling could relax our “baseline” assumptions regarding the relationship between eggs incubated and parental fitness, our study already comprises sufficiently diverse examples to point out that differences in ecological and social circumstances, such as relatedness and egg recognition, may completely switch the nature of CBP interactions from cooperation to conflict (parasitism) and vice versa.

Relatedness also facilitated host clutch reduction, a phenomenon so far only described in a limited number of studies (Andersson and Eriksson 1982; Erikstad and Bustnes 1994; Lyon 1998; Jaatinen, Jaari et al. 2009). This behavior evolved when postlaying care was relatively cheaper than egg laying and hosts and parasites were related (Figure 3A). In our results, the proportion of host eggs in the nest decreased, whereas the total number of eggs cared for remained the same (Figure 3C). The evolution of clutch reduction is in line with the study of Lyon (1998), who was the first to show that nesting parasites may benefit from laying less in their own nest and switching to parasitic laying. Our model showed that nesting parasites that laid more parasitic eggs laid fewer eggs in their own nests. However, this should not be termed a “clutch reduction” strategy because it reflects a redirection of eggs into the nests of others rather than a reduction in the total number of eggs laid. We only found true clutch reduction as a response to parasitism when relatedness was positive (depicted by the difference in the number of egg laid in the own nest between $r = 0$ and $r = 0.5$), adding to the evidence for the possibility of cooperation within CBP

strategies. True host clutch reduction as a response to parasite relatedness has to our knowledge only been described by one empirical study so far (Jaatinen, Jaari et al. 2009), a study in which we were able to monitor the total number of eggs laid by hosts, including eggs laid parasitically.

Costs of egg laying versus postlaying care

The relative costs of egg laying versus postlaying care influenced all 3 reaction norms of the strategies studied (Figure 6A–C). As costs of postlaying care increased, low- and medium-quality individuals markedly reduced the number of eggs cared for, whereas high-quality individuals were less sensitive to this cost. Quality variation may thus mask life-history trade-offs, with the best individuals achieving high fitness levels seemingly unaffected by the costs incurred (Yoccoz et al. 2002; Kim and Monaghan 2005; Hamel et al. 2009).

All else being equal, costly egg laying should lead to a focus on own nesting and reduced parasitism. These results also bear more subtle implications for the relationship between the costs of nesting and the prevalence of parasitism. In a very interesting case, we found that the benefits from cooperative CBP among relatives may be outweighed by a high cost of postlaying care, rendering the costs of receiving extra eggs higher than the potential inclusive fitness benefits (Figure 5). This result is in line with those of Andersson (2001), pointing out the robustness of the finding and highlighting the importance of breeding costs in shaping CBP strategies. The presence of both relatedness and recognition do not, by themselves, guarantee cooperative behavior. American coot parents suffer a great deal from rearing extra young, as every foreign young reared implies, on average, that one own young will perish (Lyon 2003b). The presence of highly developed defenses against parasitism and the absence of cooperative CBP are hardly surprising when one takes into account the absence of relatedness (Lyon 1993b) and the presence of highly costly postlaying parental care in this species (Lyon 2003b; note that in our model, the cost of parasitism is realized as lower adult survival, whereas American coots pay the cost immediately as reduced offspring survival).

Natal philopatry

Sex ratio theory predicts that individuals could limit harmful local competition by decreasing the production of the competing sex. However, because our model assumes a 1:1 primary sex ratio, this can only be achieved by lowering total productivity. We indeed observed a slight trend toward a lowered egg production in our results when we included local competition among females.

As noted by Franks (1998), population viscosity (sensu Queller 1994) caused by natal philopatry may outweigh the potential benefits of kin-selected cooperation. In our model, cooperative CBP did emerge as a tactic in the presence of relatedness, even if natal philopatry increased competition among females. This result does not mean that competition can never outweigh cooperative benefits; however, the scale at which local competition operates matters for the evolution of altruistic behavior (Franks 1998). Extensions to our model could thus usefully investigate this phenomenon by varying the shape of Equation 9 or, alternatively, through more explicit treatment of space.

Model limitations

Our model takes a relatively simplistic view on egg recognition and relatedness. We have assumed that individuals evolve according to average relatedness experienced in their local surroundings. Thus, our model does not include kin recognition,

which would allow hosts to treat parasitic eggs differently depending on their relatedness to the parasite (and vice versa). Kin recognition has been suggested to be present in, for example, goldeneye ducks (Andersson and Ahlund 2000). For our model that focuses on the consequences of host–parasite relatedness, it is important to note that kin recognition may underlie the positive host–parasite relatedness, which in turn influences the inclusive fitness benefits of CBP (Andersson 2001; López-Sepulcre and Kokko 2002). Nevertheless, a more explicit treatment of kin recognition may be important for future work, especially for deriving predictions for natural populations where relatedness between individuals varies strongly (Komdeur and Hatchwell 1999; Ostrowski et al. 2008). A future model incorporating kin recognition with the factors described in this study would shed more light on the accuracy of kin recognition mechanisms and their impact on the emerging CBP strategies.

Similarly, our modeling results show that individual quality is central for the shaping of CBP strategies. In our model, quality does not vary over time, which it may do in nature, for example, Individuals stressed by breeding in 1 year may have reduced resources available for reproduction in the following year (e.g., Milonoff et al. 2004). Furthermore, our model assumes parasitism to be dependent on parasite quality but random with respect to host quality. In nature, however, parasites may be able to recognize host quality and target high-quality individuals. This has been found in an interspecific brood parasite (Parejo and Aviles 2007). Cowbirds eavesdrop on potential hosts' singing, and based on the song, they choose higher quality hosts who will provide better care for the parasitic egg. Similarly, parasitic goldeneyes have been found to detect safe neighborhoods and preferentially parasitize hosts there in order to enhance the success of their parasitically laid offspring (Pöysä 2006; Pöysä and Pesonen 2007). Models including temporally varying individual quality and predation danger assessment may provide insightful for future research.

Another important simplification of our study is that we model CBP as a 2-player game. Interactions in nature are more akin to an *n*-person game, with prospects for far more complicated dynamics. Also, we have not incorporated the possibility of nest desertion in this model, and we allow individual eggs to be discarded. Nest desertion is a common response to CBP, however (e.g., Jaatinen, Öst et al. 2009), and the number of interacting females may affect patterns of parasitism and subsequently nest desertion. We therefore encourage future studies to pursue the study of CBP with respect to several interacting females and the possibility of nest desertion.

The complexity and number of mechanisms proposed to account for CBP (Lyon and Eadie 2008) mean that theoretical work has to deal with a large number of parameters. Despite the consequent shortcomings described above, the insights gained from our integrative effort should encourage future theoretical studies to continue this work by focusing on kin recognition, host choice. Similarly, our work emphasizes the need for empirical work to study CBP strategies with respect to individual quality and the relative costs of egg laying and postlaying care.

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