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Host life-history strategies and the evolution of chick-killing by brood parasitic offspring

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Nestling brood parasites vary in the harm that they do to their companions in the nest. Here we use a game-theoretical model to attempt to account for this variation. Our model considers hosts that might routinely abandon single nestlings, regardless of whether they are host young or brood parasites and choose instead to reallocate their reproductive effort to future breeding. The nestling brood parasite must decide whether or not to kill all host young by balancing the benefits it stands to gain from reduced competition in the nest against the risk of desertion by host parents. The model predicts that 3 different types of evolutionarily stable strategies can exist. 1) When hosts routinely rear depleted broods, the brood parasite always kills host young, and the host never then abandons the nest. 2) Conversely, when adult survival after deserting single offspring is very high, hosts always abandon broods of one young, and the parasite never kills host offspring. 3) Intermediate strategies can also be evolutionarily stable, in which parasites sometimes kill their nest mates, and host parents sometimes desert nests that contain only a single chick. We provide quantitative descriptions of how the values given to ecological and behavioral parameters of the host-parasite system influence the probability of each strategy and compare our results with host–brood parasite associations seen in nature.
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The obligate avian brood parasites lay their eggs in nests belonging to other species, and their victims then care for the parasitic offspring by incubating the egg and feeding the nestling (Davies 2000). This habit of exploitation is now thought to have evolved 6 times independently within the birds: in the old world cuckoos, the *Clamator* cuckoos, the new world cuckoos, the honeyguides, the *Vidua* finches, and the cuckoo-finch, *Anomalospiza imberbis*, and 5 species of cowbird (Sorenson and Payne 2002). The reproductive biology of these 100 or so brood parasites is broadly similar between species, but the behavior of their chicks differs in one key respect. Soon after hatching, the old world cuckoos, some of the new world cuckoos, and the honeyguides deliberately kill the (host) young with whom they share the nest, either by evicting them from the nest or by using their hooked bills to inflict lethal injuries (Davies 2000). In the remaining species, however, brood parasitic young are more benign and at least one of their companions in the nest commonly survives to fledge. Although these brood parasites can be responsible for the death of some host young, often because they outcompete them for food, it is not clear whether their effect on host mortality is strategic or accidental. Redondo (1993) suggests that great spotted cuckoo, *Clamator glandarius*, chicks raised in magpie, *Pica pica*, nests strategically beg at dishonestly high rates to hasten the starvation of the magpie chicks with whom they are reared. By contrast, the success of cowbird nestlings in outcompeting host young seems to be an accident of their relatively large size (e.g., Hauber 2003a; Lichtenstein and Dearborn 2004).

How can we account for such marked variation between species in the virulence of brood parasitic young? One approach is to suggest that destroying potential rivals for host resources is generally beneficial for the parasitic nestling, and so the species that lack this capability stand to gain no benefits by killing host young (because host young are not rivals for food e.g., Soler 2002), are suffering from evolutionary lag, or are constrained in some way, perhaps by the relatively large size of host young (Grim 2006c). The evidence for evolutionary lag initially seems compelling because the brood parasites belonging to more recently evolved lineages (the parasitic cowbirds and finches, Sibley and Ahlquist 1990) also tend to be those that lack offspring-killing behaviors (Davies 2000). However, there are exceptions to this rule, which suggest that it cannot fully account for the observed distribution of host killing across brood parasitic species. For example, the brown-headed cowbird *Molothrus ater* may at times strategically evict host offspring from the nest (Dearborn 1996). Furthermore, 2 old world cuckoo species, the Asian koel *Eudynamis scolopacea* and the channel-billed cuckoo *Scythrops novaehollandiae* seem to have secondarily lost the capacity to kill young because their closest living relatives (according to Sorenson and Payne 2005) are active chick-killers (Payne 2005). The hosts of these cuckoos are among the largest to be exploited by brood parasites, and it might be argued, therefore, that these cuckoo chicks simply lack the physical strength to throw host young from the nest (Krüger and Davies 2004). However, both common cuckoo, *Cuculus canorus*, and Horsfield's bronze-cuckoo, *Chalcites basalis*,chicks nestlings are capable of evicting eggs or nestlings of more than twice their body weight (Payne RB and Payne LL 1998; Davies 2000; Langmore NE and Kilner RM, unpublished data). Because the *Vidua* and cowbird hosts are typically far less than twice the mass of their parasites, it is unlikely that physical strength alone limits their capacity to kill host young (Kilner 2006). Nest structure may further restrict the ability to kill host young by eviction but is unlikely to prevent the evolution of chick-killing by other means (Kilner 2006).

An alternative line of reasoning, and the one that we explore in this paper, is to consider the possible costs that

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parasitic offspring may experience when they kill nest mates, which might limit the evolution of host-chick killing (Kilner 2005). Three types of costs might follow from the destruction of companions in the nest. First, brood parasitic young might lose kin if their mothers are in the habit of laying repeatedly in the same host nest (e.g., Martinez et al. 1998). Second, the parasitic nestling might lose assistance in soliciting care (Lotem 1998; Kilner 2003; Kilner et al. 2004). Host young might be beneficial in this regard either because they communicate more effectively than foreign young with host parents (Payne et al. 2001) or because collectively a brood of young birds presents a more potent stimulus to a provisioning parent than a lone nestling ever can (Kilner et al. 1999). A third potential cost incurred by killing nest mates is an increased risk of desertion by the host parents (e.g., Langmore et al. 2003), and this is the focus of our interest here. Specifically, we wish to construct a mathematical model to explore the logical plausibility of this factor alone in producing the observed variation in parasite chick behavior. This is not to suggest that we expect this to be the only (or even the dominant) factor driving this variation but rather that we need to evaluate its logical feasibility in order to evaluate the usefulness of future empirical investigation by manipulative experiment or comparative analysis.

When parasitic young kill all the other offspring in the nest, they reduce the brood size to one. Host parents may then choose to desert the parasitic chick, not necessarily as a coevolved response to brood parasitism but as part of a life-history strategy to avoid wasting time and effort raising a single nestling. According to this view, hosts will desert all unprofitable single chick broods, even those containing their own offspring. There is ample empirical evidence of desertion of reduced broods (summarized in Verboven and Tinbergen 2002). If host parents are following this life-history strategy to maximize their lifetime fitness, then the conditions under which nest-mate killing will evolve in young brood parasites become limited. Our aim here is to identify those conditions by using the evolutionarily stable strategy (ESS) approach to analyze a game between parasites and their hosts. Parasitic chicks choose whether or not to kill by balancing the benefits of removing the competition for host resources with the likelihood of subsequent desertion, whereas host parents choose whether or not to desert by balancing the value of continuing investment in the current brood against breeding again in the future. We aim to find the evolutionarily stable combinations of strategies for the parasite chick (whether or not to kill) and the host adult (whether or not to desert). Importantly, the host bird's decision to desert does not depend on its ability to recognize the cuckoo chick as foreign [see Grim et al. (2003) for an example of rejection without recognition]. Indeed, a fundamental assumption of the game is that the host cannot tell with certainty whether it has been parasitized or not.

MODEL DESCRIPTION

We assume a population of parasites preying on a population of hosts. For each host, the sequence of events is as follows:

1. The host bird forms a nest and lays a clutch of eggs.
2. The number of offspring in the nest can be reduced to 1 by either of 2 possible mechanisms. Firstly, a parasitic egg may be laid in the nest (this happens with probability P), and the parasitic chick can choose to kill all the other eggs or chicks (which occurs with probability C_p). Secondly, the number of chicks can be reduced to 1 by an external event unconnected with parasitism, such as predation, which occurs with probability E. It is theoretically possible that both these events could occur for the same clutch, when the order of events would be important. However, if the occurrence of parasitism and of such external events is rare, then the probability of both events occurring is very small, and for the sake of simplicity, we shall assume this is so and that only one of these events can occur. Thus, with probability $E + PC_p$, the brood will be reduced to a single individual, with probability $P(1 - C_p)$ the brood will be increased by a single (parasitic) individual beyond its original size, and with probability $1 - P - E$, the brood size will remain unchanged. Although some brood parasite females remove a host egg when laying their own, this complication does not change the conclusions of our model materially (because we do not assume any number discriminating ability from host adults other than the ability to differentiate between "one" and "several") and has been left out to aid clarity and simplicity.
3. The host must choose whether to desert the nest or not. We assume that the parent cannot detect parasitic eggs or chicks and cannot accurately detect if it has been parasitized or not. It can tell only if there is a single chick in the nest or more than one (perhaps using begging rate or gape area as indicators).
4. If there is more than one (which could be a full brood of its own young or a full brood of its own young plus a parasite), then it does not desert; if there is a single chick (which could be its own or a parasite) then it deserts with probability C_h and does not desert with probability $1 - C_h$.

The rewards from a given breeding attempt are described by a set of 3 parameters; the first is the payoff to the host from offspring in its nest, the second is the payoff to the parasite, and the third is the probability of the parent surviving the winter to breed again next year. There are 6 possibilities, as defined in Table 1. The table also introduces the remaining variables needed to fully define the model. We can impose some limitations on the values taken by these variables on biological grounds.

We assume that the parasite's fitness would be higher if it did not suffer competition from the host chicks. We define ϕ as the value (to its parent) of a parasite brought up with a brood of host chicks, relative to one brought up alone, so we can assume $0 < \phi < 1$ (but see Kilner et al. 2004). We also assume that competition with the parasite would be detrimental to host chicks. We define c as the value of a brood of chicks (to the host parent) brought up with a parasite chick compared with being brought up without the parasite, so $0 < c < 1$. Raising a full brood should be better for the parent than raising a single one of its chicks. We define B as the value of a full brood relative to the value of a single host chick and so

Table 1

The rewards from a given breeding attempt, described by a set of 3 parameters: the first is the payoff to the host, the second is the payoff to the parasite, and the third is the probability of the parent surviving to breed again

Probability	Description	Payoff
$1 - P - E$	No parasitism occurs	B, -, μ_b
$P(1 - C_p)$	Parasitism occurs but without ejection	cB, ϕ, μ_{bp}
EC_h	A lone host chick is deserted	0, -, μ_d
$E(1 - C_h)$	A lone host chick is not deserted	1, -, μ_s
PC_pC_h	A lone parasite chick is deserted	0, 0, μ_d
$PC_p(1 - C_h)$	A lone parasite chick is not deserted	0, 1, μ_p

Notice that where no parasitism occurs, there is no payoff to the parasite, and so the second element of the set is denoted by a "-."

$B > 1$. Implicit assumptions of our fitness measure are that density dependence acts through juvenile survival alone and that we interpret the payoffs of 1 and B for one offspring and the whole brood, respectively, to be proportional to survival (with the constant of proportionality depending on other parameters through density dependence).

The greatest chance of host adult overwinter survival is given by desertion, raising a single chick will certainly not lead to a greater chance of survival, and may lead to a smaller chance. In turn, raising a full brood of its own offspring will not lead to greater survival than raising a single one of these offspring and may lead to reduced survival. Raising both a brood and a parasite will not allow greater survival than raising a full brood and may well reduce survival. From these assumptions, we get

$$\mu_{\mathrm{bp}} \leq \mu_{\mathrm{b}} \leq \mu_{\mathrm{s}} \leq \mu_{\mathrm{d}},$$

where μ_{bp} is the probability of host survival after raising a full brood and a parasite, μ_{b} is the probability of host survival after raising a full brood, μ_{s} denotes the probability of survival after raising a single host chick, and μ_{d} is the probability of host survival after desertion of the reduced brood.

Similarly, if the parasite chick is larger than a host chick, raising a single parasite will not increase adult survival compared with raising a single host chick and may well decrease survival. Finally, raising a parasite alongside a full brood will not lead to greater survival than raising only a parasite and may well decrease survival. Thus, we have

$$\mu_{\mathrm{bp}} \leq \mu_{\mathrm{p}} \leq \mu_{\mathrm{s}} \leq \mu_{\mathrm{d}},$$

where μ_{p} is the probability of host survival after raising a single parasite.

One important point about these relations is that we make no assumptions about the survivorship consequences of raising a parasite compared with a full brood of host chicks, that is, we make no assumption about the relative values of μ_{p} and μ_{b}.

ANALYSIS TO DETERMINE ESSs

We want to find equilibrium strategy pairs (C_{h},C_{p}) where either party cannot increase their reward by changing strategy. We will also look at the stability of any equilibria.

We shall consider the reward $R(C_{\mathrm{h}},C_{\mathrm{p}})$ to a host individual using strategy C_{h} in a population of parasites all using strategy C_{p} and the reward $S(C_{\mathrm{p}},C_{\mathrm{h}})$ to a parasite individual using strategy C_{p} in a population of hosts using C_{h}. It is possible that there is more than one strategy of either host or parasite present in the population, in which case we must extend the above notation, as when we check the stability of our solutions (see Appendix B).

The reward for a parasite (S) is much simpler to calculate because it is just the reward from a single interaction. It is given by

$$S(C_{\mathrm{p}}, C_{\mathrm{h}}) = \phi(1 - C_{\mathrm{p}}) + C_{\mathrm{p}}(1 - C_{\mathrm{h}}) = \phi + C_{\mathrm{p}}(1 - \phi - C_{\mathrm{h}}). \quad (1)$$

The reward for the host (R) is more complicated because the host potentially takes part in a number of different breeding attempts. So for each case of the current breeding attempt, the reward is that from the current attempt plus the overall expected reward from the subsequent attempt multiplied by the chance of surviving to this next breeding attempt. Thus, if R_i is the value of the expected reward to a host of age i, we would obtain an expression in terms of R_{i+1}, its expected reward in the subsequent year. The best strategy would then depend on the age of the individual. We simplify this by setting $R_i = R$ for all i, and so the expected reward for the subsequent attempt is just R.

Note that our analysis will only work for a stable population. If population size changes with time, then the value of a brood depends on when it is raised (e.g., for increasing populations, an earlier brood is better than a later one) and analysis would be more complex for any realistic version of such a model, which would have to have density-dependent rewards. We would perhaps have to use a simulation model.

Thus,

$$\begin{aligned} R = {} & (1 - P - E)(B + R\mu_{\mathrm{b}}) + P(1 - C_{\mathrm{p}})(cB + R\mu_{\mathrm{bp}}) \\ & + EC_{\mathrm{h}}\mu_{\mathrm{d}}R + E(1 - C_{\mathrm{h}})(1 + \mu_{\mathrm{s}}R) + PC_{\mathrm{p}}C_{\mathrm{h}}\mu_{\mathrm{d}}R \\ & + PC_{\mathrm{p}}(1 - C_{\mathrm{h}})\mu_{\mathrm{p}}R. \end{aligned} \quad (2)$$

This can be rearranged to give

$$\begin{aligned} R(C_{\mathrm{h}}, C_{\mathrm{p}}) = {} & [(1 - P - E)B + PcB + E - PcBC_{\mathrm{p}} - EC_{\mathrm{h}}]/ \\ & [1 - \mu_{\mathrm{b}} + P(\mu_{\mathrm{b}} - \mu_{\mathrm{bp}}) + E(\mu_{\mathrm{b}} - \mu_{\mathrm{s}}) + PC_{\mathrm{p}}(\mu_{\mathrm{bp}} - \mu_{\mathrm{p}}) \\ & + EC_{\mathrm{h}}(\mu_{\mathrm{s}} - \mu_{\mathrm{d}}) + PC_{\mathrm{p}}C_{\mathrm{h}}(\mu_{\mathrm{p}} - \mu_{\mathrm{d}})]. \end{aligned} \quad (3)$$

For an equilibrium pair (C_{p}^*, C_{h}^*), we need that C_{h}^* maximizes $R(C_{\mathrm{h}}, C_{\mathrm{p}}^*)$ and C_{p}^* maximizes $S(C_{\mathrm{p}}, C_{\mathrm{h}}^*)$ so that in a population where every host uses strategy C_{h}^* and every parasite uses strategy C_{p}^*, there is no strategy change by either host or parasite that can improve fitness.From Equation 1,

$$S(C_{\mathrm{p}}, C_{\mathrm{h}}^*) = \phi + C_{\mathrm{p}}(1 - \phi - C_{\mathrm{h}}^*). \quad (4)$$

By inspection, we can see that if $C_{\mathrm{h}}^* = 1 - \phi$, then S is independent of C_{p}. If $C_{\mathrm{h}}^* < 1 - \phi$, then S is maximized when $C_{\mathrm{p}} = 1$, and when $C_{\mathrm{h}}^* > 1 - \phi$, then S is maximized by $C_{\mathrm{p}} = 0$.

Thus, this system can have 3 types of equilibrium:

1. One where the parasite always kills ($C_{\mathrm{p}}^* = 1, C_{\mathrm{h}}^* < 1 - \phi$)
2. One where the parasite never kills ($C_{\mathrm{p}}^* = 0, C_{\mathrm{h}}^* > 1 - \phi$)
3. An intermediate case where all parasitic strategies are equally successful ($0 \leq C_{\mathrm{p}}^* \leq 1, C_{\mathrm{h}}^* = 1 - \phi$).We can rewrite Equation 3 as

$$R(C_{\mathrm{p}}, C_{\mathrm{h}}) = \frac{\alpha + \beta C_{\mathrm{h}}}{\gamma + \delta C_{\mathrm{h}}}, \quad (5)$$

where

$$\alpha = (1 - P - E)B + PcB + E - PcBC_{\mathrm{p}}^*, \quad (6)$$

$$\beta = -E, \quad (7)$$

$$\gamma = (1 - \mu_{\mathrm{b}}) + P(\mu_{\mathrm{b}} - \mu_{\mathrm{bp}}) + E(\mu_{\mathrm{b}} - \mu_{\mathrm{s}}) + P(\mu_{\mathrm{bp}} - \mu_{\mathrm{p}})C_{\mathrm{p}}^*, \quad (8)$$

and

$$\delta = E(\mu_{\mathrm{s}} - \mu_{\mathrm{d}}) + PC_{\mathrm{p}}^*(\mu_{\mathrm{p}} - \mu_{\mathrm{d}}). \quad (9)$$

From this, it is easy to show that

$$\frac{\partial R}{\partial C_{\mathrm{h}}} = \frac{\beta\gamma - \alpha\delta}{(\gamma + \delta C_{\mathrm{h}})^2}. \quad (10)$$

Thus, if $\beta\gamma > \alpha\delta$, then R increases with C_{h} and so $C_{\mathrm{h}}^* = 1$, whereas if $\beta\gamma < \alpha\delta$, then R decreases with C_{h} and so $C_{\mathrm{h}}^* = 0$. In the boundary case where $\beta\gamma = \alpha\delta$, then R is constant for C_{h} and any $0 \leq C_{\mathrm{h}}^* \leq 1$ is possible.

In order to make further progress, we need to describe $\beta\gamma - \alpha\delta$ as a polynomial in C_p^*. With some manipulation it is possible to show that

$$\beta\gamma - \alpha\delta = G_0 + G_1 C_p^* + G_2 (C_p^*)^2, \tag{11}$$

where

$$\begin{aligned} G_0 = {} & E(-(1 - \mu_b) + P(\mu_{bp} - \mu_b) + E(\mu_d - \mu_b) \\ & + B(\mu_d - \mu_s)(1 - P - E + cP)), \end{aligned} \tag{12}$$

$$\begin{aligned} G_1 = {} & (\mu_d - \mu_{bp})EP + (\mu_s - \mu_d)PcBE \\ & + (\mu_d - \mu_p)PB(1 - P - E + cP), \end{aligned} \tag{13}$$

and

$$G_2 = P^2 cB(\mu_p - \mu_d). \tag{14}$$

Thus, possible ESS solutions include the case where the parasite always evicts host eggs and the host never abandons the nest ($C_p^* = 1; C_h^* = 0$). This occurs when $\beta\gamma - \alpha\delta < 0$, that is, when $G_0 + G_1 + G_2 < 0$.

It is also possible to get solutions where the parasite never ejects host chicks and the host always abandons the nest if it has one chick in it ($C_p^* = 0; C_h^* = 1$). This occurs when $\beta\gamma - \alpha\delta > 0$, that is, when $G_0 > 0$. The outcome of this strategy in a real population would be a situation where parasitic chicks tolerate nest mates, and hosts raise both the parasite and their own chicks together. The hosts do desert when their brood size is drastically reduced, but this occurs only through external events such as predation and not through chick-killing by parasites.

Cases where C_p^* equals 1 or 0, but C_h^* does not equal either 0 or 1, require very specific combinations of parameters such that either $G_0 = 0$ or $G_0 + G_1 + G_2 = 0$. It is highly improbable that any natural system would have exactly the correct combination of parameter values to give such solutions, so they are not considered any further.

Hence, we now turn to intermediate solutions where C_p^* is neither 0 nor 1, that is, where $0 < C_p^* < 1$. For this, we need

$$C_h^* = 1 - \phi. \tag{15}$$

This can only occur if $\beta\gamma - \alpha\delta = 0$. That is, solutions of the form ($0 < C_p^* < 1; C_h^* = 1 - \phi$) can only occur at the roots of

$$G_0 + G_1 C_p^* + G_2 (C_p^*)^2 = 0. \tag{16}$$

At first sight, Equations 15 and 16 also appear to require a precise coincidence of parameters. However, satisfying Equations 15 and 16 is not implausible biologically in the same way as above because they involve the strategies played by the birds themselves, and natural selection may cause the strategies in the population to evolve to such particular values. We define the function

$$f(x) = G_2 x^2 + G_1 x + G_0, \tag{17}$$

and we are interested in roots of this function within the interval (0, 1). We can see by inspection that $G_2 < 0$, and thus $f(x) \to -\infty$ as $x \to \pm\infty$, and there is a unique turning point (given by $2G_2 x + G_1 = 0$), which is a maximum. There are 7 different ways in which $f(x)$ can lie in relation to the interval $x \in [0, 1]$: see Figure 1. From our previous arguments, if $f(0) > 0$, then the $C_p^* = 0$ ESS occurs, and if $f(1) < 0$, then the $C_p^* = 1$ ESS occurs. We are also interested in intermediate equilibria that may occur when $f(x) = 0$ for any $0 < x < 1$. Some of these equilibria are stable, and some are not.

For cases (i), (ii), and (iii) of Figure 1, $C_p^* = 1$ is the unique ESS.

For case (iv), $C_p^* = 0$ is the unique ESS.

For case (v), both $C_p^* = 0$ and $C_p^* = 1$ are ESSs, and there is a single intermediate solution.

For case (vi), neither $C_p^* = 0$ nor $C_p^* = 1$ are ESSs, but there is a single intermediate solution.

For case (vii), $C_p^* = 1$ is an ESS, and there are 2 intermediate solutions.Which of these 7 cases occurs depends on

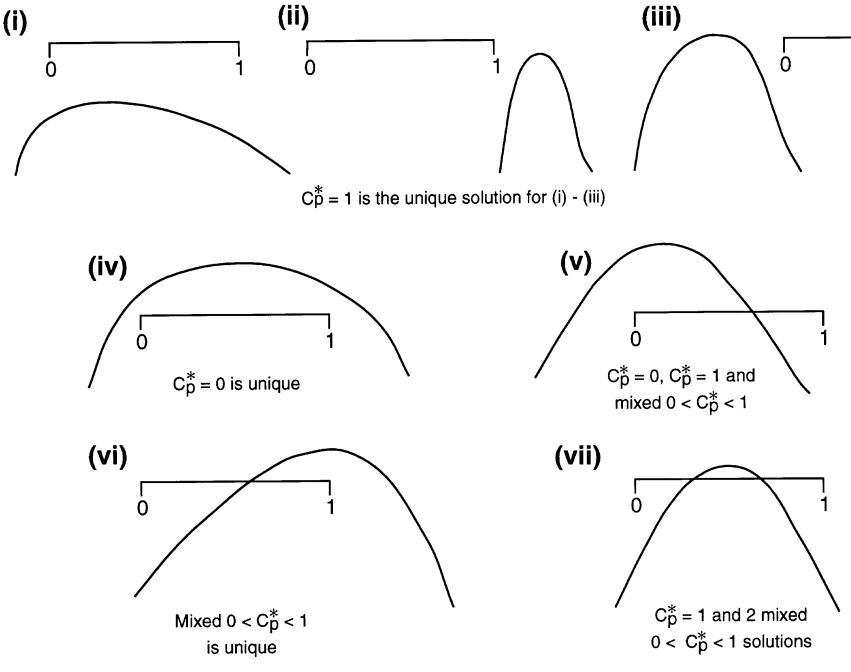

Figure 1
A generic depiction of the possible values of the function $f(x)$ from Equation 17 over the range [0, 1], which yields the ESSs for each case, which are summarized in Table 2.

the values of G_0, G_1, and G_2. For there to be any, x such that $f(x) = 0$, we need ${G_1}^2 > 4G_0G_2$ (we ignore the highly biologically unlikely case where parameter values are such that $G_1^2 = 4G_0G_2$). This gives 2 roots R_s and R_l, where $R_s < R_l$;

$$R_s = \frac{-G_1 + \sqrt{G_1^2 - 4G_0G_2}}{2G_2} \tag{18}$$

and

$$R_l = \frac{-G_1 - \sqrt{G_1^2 - 4G_0G_2}}{2G_2}. \tag{19}$$

We are interested in cases only where these roots fall within (0, 1). In Appendix A, it is shown that 5 criteria determine which of the 7 cases that a given set of parameter values falls into:

$$\text{(A)}\ G_1^2 > 4G_0G_2, \tag{20}$$

$$\text{(B)}\ G_0 > 0, \tag{21}$$

$$\text{(C)}\ G_1 > 0, \tag{22}$$

$$\text{(D)}\ G_1 + 2G_2 > 0, \tag{23}$$

$$\text{(E)}\ G_0 + G_1 + G_2 > 0. \tag{24}$$

If (A) is not satisfied, then (regardless of whether the other conditions are met or not), $C_p^* = 1$ is the unique ESS [Figure 1, case (i)]. Hence, we concentrate on cases where (A) is met. There are 16 possible combinations for the remaining 4 conditions either to be met or not. These combinations are summarized in Table 2.

From our previous arguments, it can be seen that where they exist, the $C_p^* = 0$ and $C_p^* = 1$ equilibria are always evolutionarily stable. We demonstrate the stability (or otherwise) of all intermediate equilibria in Appendix B, which shows that solutions that cross the y-axis when $f(x)$ is decreasing (the solutions associated with R_l) are unstable, whereas those for which it is increasing (the solutions associated with R_s) are stable. This means that the intermediate solutions in cases (4) and (8) of Table 2 are unstable, as is the larger of the intermediate solutions in case (12). All other intermediate equilibria (i.e., cases 9, 11, and the lower value in 12) are stable.

Hence, for a given set of parameter values, we find the ESS value (or values) of C_p^* by calculating first G_0, G_1, and G_2, then each of the 5 criteria (A–E), and then consulting Table 1. Where there is a stable intermediate value, then R_s needs to be calculated using (18).

Once the ESS value of C_p is found, then the ESS value of C_h can be found easily. If $C_p^* = 1$, then $C_h^* = 0$, if $C_p^* = 0$ then $C_h^* = 1$, otherwise $C_h^* = 1 - \phi$. The relationship between specific parameter values and given ESSs needs to be explored numerically.

PLAUSIBLE PARAMETER VALUES

In order to explore the model's predictions further, we need to understand how the values given to parameters translate into ESS behaviors of parasite and host. For this, we need to consider plausible parameter values.

First, we have the probabilities of parasitism (P) or egg loss through external factors (E). These must both be nonnegative, and $E + P$ must be ≤ 1. We will assume default values of 0.15 for each. E varies strongly between species, populations, and even years, so the value of 0.15 is plausible, but perhaps more relevant to cavity nesters than open-nesting species where higher predation rates may be expected (Nilsson 1986). P values of 0.15 are likely to be quite high for cuckoos, or the common cuckoo at least. In most of Europe, its parasitism rate is 3–8% (Davies 2000; Payne 2005). However, we adopt this value because it is approximately the maximum for which our assumption (implicitly in point 2 of the model description) that the probability of 2 parasites selecting the same nest is negligible can be justified (see Honza and Moskat 2005).

Table 2
If (A) is not satisfied$_p$, $C_p^* = 1$ is the unique ESS

	B	C	D	E		Figure 1
1	Y	Y	Y	Y	$C_p^* = 0$ is the unique ESS	(iv)
2	Y	Y	Y	N	This combination is impossible to achieve	—
3	Y	Y	N	Y	$C_p^* = 0$ is the unique ESS	(iv)
4	Y	Y	N	N	Both $C_p^* = 0$ and 1 are ESS + an intermediate unstable equilibrium	(v)
5	Y	N	Y	Y	This combination is impossible to achieve	—
6	Y	N	Y	N	This combination is impossible to achieve	—
7	Y	N	N	Y	$C_p^* = 0$ is the unique ESS	(iv)
8	Y	N	N	N	Both $C_p^* = 0$ and 1 are ESS + an intermediate unstable equilibrium	(v)
9	N	Y	Y	Y	There is a stable intermediate equilibrium only	(vi)
10	N	Y	Y	N	$C_p^* = 1$ is the unique ESS	(ii)
11	N	Y	N	Y	These is a stable intermediate equilibrium only	(vi)
12	N	Y	N	N	$C_p^* = 1$ is an ESS + 2 intermediate equilibria, one stable, the other not	(vii)
13	N	N	Y	Y	This combination is impossible to achieve	—
14	N	N	Y	N	This combination is impossible to achieve	—
15	N	N	N	Y	This combination is impossible to achieve	—
16	N	N	N	N	$C_p^* = 1$ is the unique ESS	(iii)

Where (A) is met, there are 16 possible combinations for 4 conditions either to be met (denoted "Y") or not met (denoted "N"). These combinations are described along with the possible solutions that each allows and the part of Figure 1 that each relates to.

The value (B) of a full brood to a parent (relative to the value of a single chick) is approximately the brood size (modified by a factor to account for, e.g., between-sib competition), so for small passerine birds, we might expect this to be between 2 and 6. We will assume a default value of 4.

There are also 2 parameters related to competition between a parasite and the host's chicks. We assume that the parasite's fitness would be higher if it did not suffer competition from the host chicks, and ϕ is the fitness value of a parasite raised in competition relative to one raised alone. This value must be between 0 and 1, and we will assume a default value of 0.7. This is likely to be a high estimate both from within-species evidence and between-species evidence (e.g., Hauber 2003a, 2003b).

We also assume that competition with the parasite reduces the fitness values of a brood of host chicks by a multiplicative factor $0 < c < 1$. Again, this value must be between 0 and 1, and we will assume a default value of 0.5 (see Hoover [2003], for data from a prothonotary warbler, *Prothonotaria citrea*, population parasitized by brown-headed cowbirds).

Lastly, we have the host adult survival probabilities, such that

$$\mu_{bp} \leq \mu_b \leq \mu_s \leq \mu_d,$$

and

$$\mu_{bp} \leq \mu_p \leq \mu_s \leq \mu_d.$$

Generally, parasite hosts are not long-lived birds so we assume default values of $\mu_d = 0.45$, with μ_b being 0.35, along with values of 0.4 for μ_s, 0.35 for μ_p, and 0.3 for μ_{bp}. The mean survival value for British cuckoo hosts (i.e., robin *Erithacus rubecula* 0.419, wren *Troglodytes troglodytes* 0.319, meadow pipit *Anthus pratensis* 0.543, pied wagtail *Motacilla alba* 0.485, and dunnock *Prunella modularis* 0.473) raising their own unparasitized broods μ_b is 0.448 (data from British Trust for Ornithology BirdFacts database: http://blx1.bto.org/birdfacts/index.htm), suggesting that our assumed default values are at least plausible.

NUMERICAL RESULTS

We varied each parameter in turn, keeping the remaining at their default values. For the default values, the ESS is for hosts never to desert single chicks ($C_h = 0$) and for parasites always to kill ($C_p = 1$).

Figure 2a shows the effect of varying B, the value of a full clutch to a host parent (relative to the value of a single host chick). There is no change in behavior until B exceeds a critical value (just below 6). Above this value, the host begins to desert, switching to its intermediate strategy of deserting a single chick with probability $(1 - \phi)$. This makes sense because as B increases, the value of future broods, relative to a current single chick, increases, and there comes a point where the fitness benefits to the host of greater survival from desertion exceed the costs of potentially deserting one of the host's own chicks. This strategy by the hosts makes killing less attractive to parasites, and so the rate at which parasites kill nest mates reduces from one. As B increases beyond this threshold, the host's strategy remains the same but (because increasing B makes desertion ever more attractive to hosts), the parasite must compensate hosts by reducing its rate of killing, so reducing the chance that a single chick in the nest is actually parasitic and hence of no fitness value to the hosts.

Figure 2b shows the effect of varying E, the probability that a host's brood is reduced to a single individual, through an external event. We find on decreasing E from the default value that there is a critical point at which the host switches to its intermediate strategy of sometimes deserting singletons. As E decreases, so the likelihood that a singleton is actually the host's own chick and not a parasite decreases, and so desertion becomes more attractive. At this point, the parasite's probability of killing declines from one, and continues to decline with decreasing E, as the parasite's strategy has to change to compensate for the increased attractiveness of desertion to the host as E (and thus, the chance that a single remaining chick is not a parasite) becomes smaller still.

Figure 2c shows no change in behavior with variation in P, the probability of parasitism. Based on the previous 2 figures, one might expect that there would be an upper critical value of P such that for values beyond this the high chance that a single individual was a parasite would induce the hosts to switch to desertion. This does not occur, firstly because there is still a chance that a singleton is the host's own chick (and therefore there is a benefit to not deserting), but also when parasitism is very high in this generation it will also be very high in the next generation, making future potential breeding attempts less valuable, and so desertion less attractive. However, it should be remembered that our model is likely to become unreliable when P is much higher than our baseline value of 0.15 because then our assumption that nests never receive more than one parasitic egg becomes difficult to justify. The arguments above do suggest, however, that our predictions are likely to be insensitive to the specific value of P, providing it is sufficiently low that this assumption is valid.

The cost of competition with the host's chicks to the parasite ϕ does not appear in G_0, G_1, or G_2 and so has no effect on which of the 3 strategy types is adopted by host and parasite. If, however, the values of other parameters mean that the intermediate strategy type is adopted, then the value of ϕ does have a quantitative effect on the strategy. This can be understood by thinking of the interaction as a game in which the host makes an initial choice and then the parasite chooses what to play based on the host's choice. There are only 3 stable host possibilities. If hosts never desert, then the parasite does best by always killing, irrespective of the value of ϕ. Similarly, if hosts always desert, then parasites should never kill, regardless of the ϕ value. However, for the intermediate solution, an interesting phenomenon occurs: low ϕ means that a parasite does worse by not killing host young but has no direct effect on the host. There seems to be a paradox here in that one might expect that the parasite would then choose to kill more often. However, this would then harm the host, so as ϕ gets smaller the host chooses a higher desertion probability, which in turn deters the parasite from killing. Thus, the value of ϕ has no effect on the parasite strategy (although it directly affects its payoff) but changes the host strategy (although it does not directly affect its payoff).

The cost of competition with a parasite to the host c does affect both G_0 and G_1. However, when all the other parameters take their default values, then the strategy adopted is independent of the value of c. When c takes its default value, parasites always kill and hosts never desert. Changing c has no effect on the host's decision because it affects neither the value of the current brood (with one chick only) nor the future broods (which will contain either one chick or a full clutch but never a full clutch and a parasite—because the parasite always kills). Changing c does not affect the parasite's decision to kill; it should always kill because the host never deserts. Changing c could have an effect on strategy if the default parameter values lead to a different strategy pair but has no effect on this particular strategy pair. For example, in Figure 2d we increase the survival probabilities such that $\mu_d = 0.75$, $\mu_b = 0.6$, $\mu_s = 0.65$, $\mu_p = 0.4$, and $\mu_{bp} = 0.3$. Now, we see that the strategy throughout is the intermediate one where the host sometimes

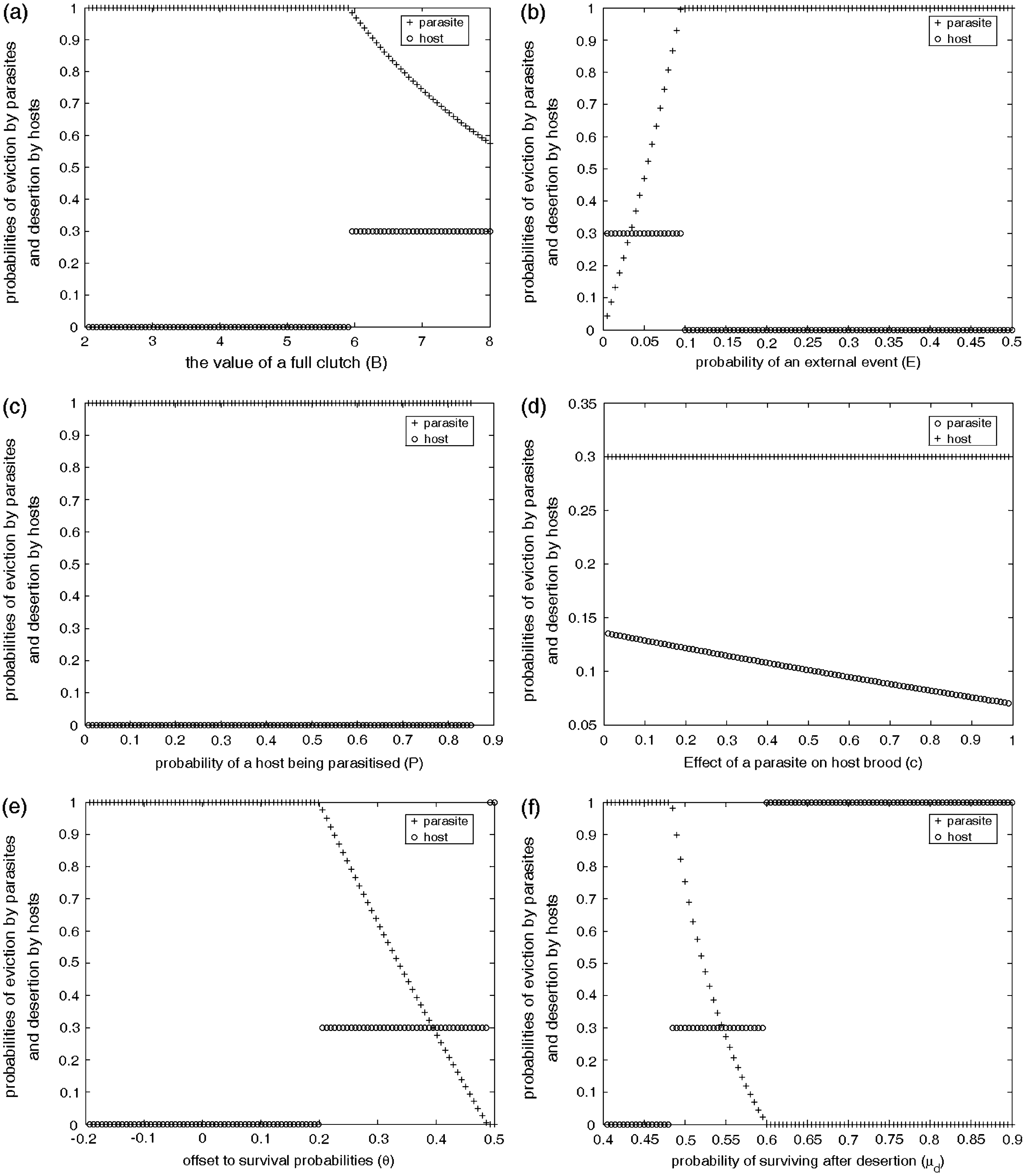

Figure 2

The effect of altering parameter values on the ESS for both parasites and hosts. The probability of the parasite killing the host's eggs or chicks, C_p, is given by the "plus" symbols, that is, $C_p = 1$ means the parasite should always kill; the probability that the host will desert a single chick, C_h, is given by the circular symbols, that is, $C_h = 1$ means the host should always desert if it finds only a single individual in its nest. Unless otherwise stated, the default parameter values are used except for the variable on the *x*-axis: these values are $P = 0.15$, $E = 0.15$, $B = 4$, $\phi = 0.7$, $c = 0.5$, $\mu_d = 0.45$, $\mu_b = 0.35$, $\mu_s = 0.4$, $\mu_p = 0.35$, and $\mu_{bp} = 0.3$. We show the consequences of varying (a) the value of a brood (B); (b) the probability of brood reduction through an external event (E); (c) the probability of parasitism (P); (d) the effect of the parasite on the host brood (c) for the default values except $\mu_d = 0.75$, $\mu_b = 0.6$, $\mu_s = 0.65$, $\mu_p = 0.4$, and $\mu_{bp} = 0.3$; (e) the between-breeding-attempt survival of the host, with all 5 default survivorship probabilities being modified by the same additive value (θ, see Numerical Results); (f) the probability of surviving after desertion (μ_d) when all other parameters take default values; (g) the probability of surviving after raising a fully unparasitized brood (μ_b) when the other survivorship probabilities are $\mu_d = 0.75$, $\mu_s = 0.65$, $\mu_p = 0.4$, and $\mu_{bp} = 0.5\mu_b$; (h) the probability of surviving after raising a lone parasitic chick (μ_p) when the other survivorship probabilities are $\mu_d = 0.75$, $\mu_s = 0.65$, $\mu_b = 0.35$, and $\mu_{bp} = 0.5\mu_p$; (i) the probability of surviving after raising a lone parasitic chick (μ_p) when the other survivorship probabilities take the default values except that $\mu_{bp} = 0.5\mu_p$ (j) the value of a full brood (B) for parameter values $\mu_d = 0.77$, $\mu_s = 0.75$, $\mu_b = 0.35$, $\mu_p = 0.35$, $\mu_{bp} = 0.3$, $E = 0.2$, $P = 0.78$, $c = 0.2$, and $\phi = 0.5$.

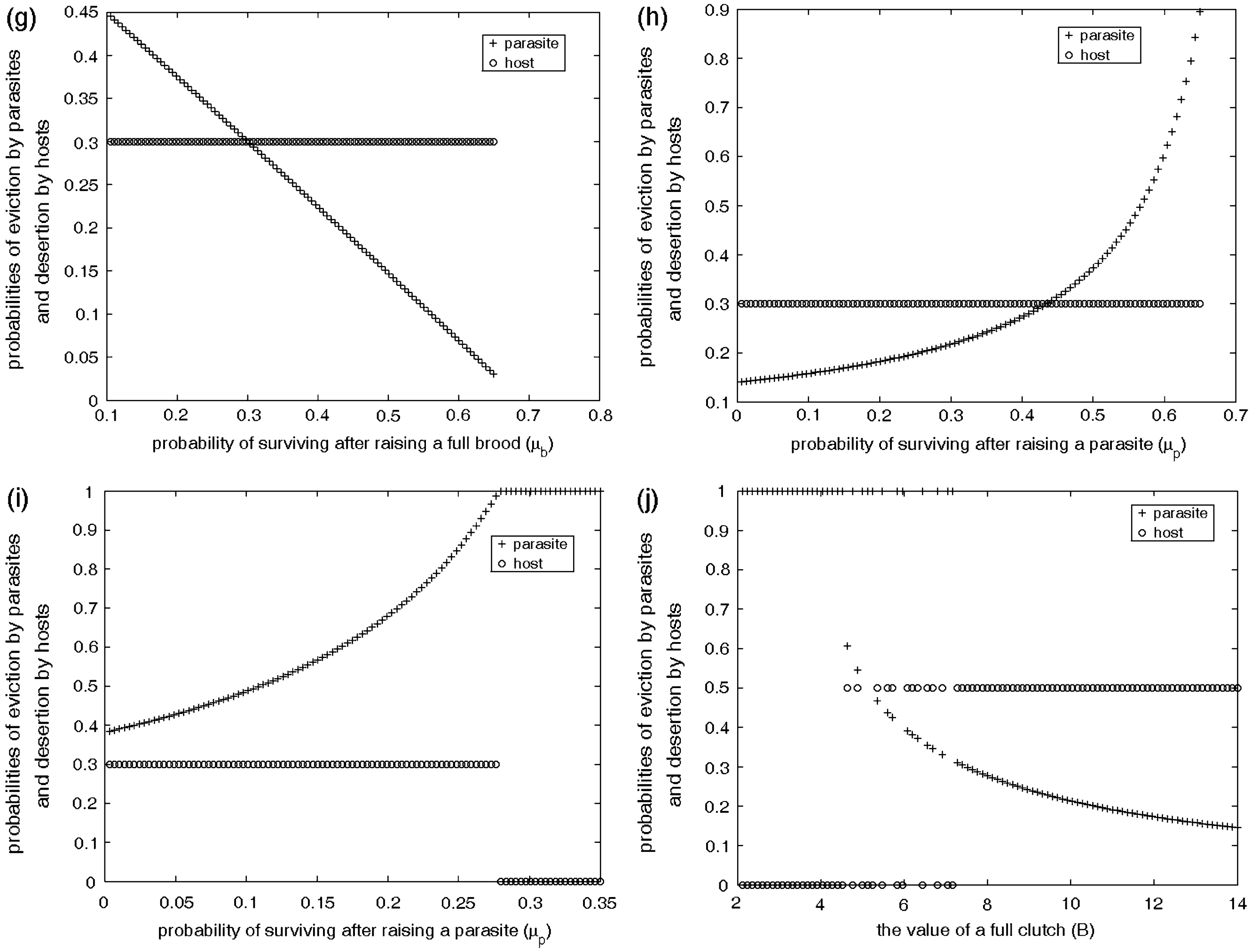

Figure 2, continued

deserts. Now, as *c* increases, the form of this strategy changes as the frequency of killing by the parasite declines. This occurs because increasing *c* makes desertion more attractive to the host because it increases the value of potential future broods. In order to compensate for this (and avoid the host switching to deserting all singletons), the parasite has to increase the value of the current brood by reducing the frequency of killing (so increasing the likelihood that the current singleton is the host's own offspring).

We can explore the effect of host longevity by adding an offset (θ) to each of the 5 default survival probabilities, with a higher value of θ indicating generally higher between-breeding attempt survivorship of a longer lived host. Increasing survival rates in this way should increase the value of future reproduction relative to the current single chick in the nest and should favor increased desertion rates by the host. This is what we see in Figure 2e, with the switch to the intermediate host strategy of sometimes rejecting occurring when the offset exceeds a value of around 0.2; for values above this the parasite's probability of chick-killing begins to decline, for similar reasons to those discussed previously. However, with high enough survivorship the rate of killing is driven down to 0, and the system flips to the unusual strategy combination of hosts that always desert and parasites that never kill. Notice that this only happens when survivorship is very high, such that the probability of surviving to the next breeding attempt is between 0.95 and 0.8. These values are generally higher than experienced by any host species. Essentially similar arguments explain the model predictions as we vary only the probability of survival after desertion in Figure 2f.

We next turn to exploring the consequences of increasing the costs of raising a full brood of chicks (by decreasing μ_b and μ_{bp}). We would expect that decreasing μ_b reduces the value of future reproductive events and so makes desertion less attractive. Because the strategy at the default values is never to desert, we would not expect this to induce a change in strategy. However, increasing μ_b might be expected to induce a strategy change by making desertion more attractive, although for the range of parameter values possible for μ_b we see no change in strategy. This occurs no matter the value given to μ_{bp}, which is not surprising because as current parasite strategy involves always killing, so the situation of raising a full brood and a parasite together would generally very rarely occur through mutation effects. If we change the values as before such that $\mu_d = 0.75$, $\mu_s = 0.65$, $\mu_p = 0.4$, and $\mu_{bp} = 0.5\mu_b$, then the intermediate strategy is predicted for the entire range of plausible values of μ_b (Figure 2g). However, as μ_b increases, desertion becomes more attractive to the host, and so the parasite's probability of killing has to decline to increase the average value of the current single chick. Conversely, when we vary the cost of rearing a parasite in Figure 2h ($\mu_d = 0.75$, $\mu_s = 0.65$, $\mu_b = 0.35$, and $\mu_{bp} = 0.5\mu_p$), we see that increasing the likelihood of survival after raising a parasite makes desertion less attractive and so allows the parasite to increase its likelihood of killing. Although it did not occur in Figure 2g,h, changing survivorship probabilities can induce a change in the form of the predicted strategy pair. If we switch back to the default parameter values, except $\mu_{bp} = 0.5\mu_p$, then Figure 2i shows that as the cost of rearing a parasite increases (i.e., μ_p declines), so desertion becomes more attractive to the host, which switches from never deserting to the intermediate desertion strategy. Further declines in μ_p cause the parasite to decline its likelihood of chick-killing.

Another prediction of the analysis was that coexisting ESSs could occur (cases [v] and [vii] from Table 2). That is, the ESS shown by a particular system would be dependent not only on the current values given to parameters (the current ecology) but also on the history of the system. Thus, 2 currently identical populations could show quite different behaviors because they have different evolutionary histories. An example of such a situation can be seen in Figure 2j. At low B values, there is a single ESS with parasites always killing and hosts never deserting. However, between B values of around 4 and 7, this ESS coexists with the intermediate ESS. For higher B values than this, then the intermediate ESS becomes the only stable state. Extensive numerical exploration suggests that coexisting ESSs are relatively uncommonly predicted and only occur when the probability of parasitism has unrealistically high values. To generate Figure 2j, the following parameter values were used: $\mu_d = 0.77$, $\mu_s = 0.75$, $\mu_b = 0.35$, $\mu_p = 0.35$, and $\mu_{bp} = 0.3$; $E = 0.2$, $P = 0.78$, $c = 0.2$, and $\phi = 0.5$. Thus, hosts are parasitized on 78% of occasions and find a single chick in their nest on 98% of occasions. If the parasitism rate is dropped to even 75%, then the multiple ESS situation disappears.

DISCUSSION

We have analyzed a model that describes how hosts might respond to the presence of a brood parasite in their nest. Most previous work has considered this problem by considering a coevolutionary arms race between the parasite and its host, in which the cost of exploitation by the parasite selects hosts that mount defences against parasitism and these, in turn, select parasites that can outwit their hosts (Rothstein 1990; Davies 2000; but see Grim et al. 2003). The principal costs of parasitism suffered by the host are sustained soon after the brood parasitic nestling hatches, when it might kill the host young. In general, when the nestling parasite is virulent, hosts are more likely to exhibit defences against parasitism, and they are most in evidence at the egg-laying stage of the breeding cycle (Davies 2000). Host adaptations for recognizing and rejecting foreign chicks are relatively rare (Lotem 1993; Langmore et al. 2003; Grim 2006a) and are most likely to be seen if parasites routinely breach the host defences mounted at the egg-stage (Planquè et al. 2002; Langmore et al. 2003; Grim 2006a).

Our different approach is to focus on the life history of the host (e.g., Soler 2002, Lyon and Eadie 2004). Whereas previous work has focused on host behavior during interactions with intraspecific brood parasites (Lyon and Eadie 2004), or during chick rearing (Soler 2002), our interest is the interaction of parasitism with life-history parameters not directly related to the nestling period, such as longevity. In our model, when hosts can gain greater fitness from future broods than they can from the continued care of a current single nestling, then their best strategy is always to give up on the current breeding attempt, regardless of whether the single chick is their own or a brood parasite. After hatching, the parasite must choose whether or not to kill host young, balancing the benefits of becoming the sole beneficiary of parental care against the risk that, as a single chick in the nest, it will be abandoned. When the risk of desertion is sufficiently high, the parasite does not kill host young, in order to guarantee its continued care.

Using the ESS approach, our model found 3 types of equilibria at which cuckoo and host strategies were evolutionarily stable. In the first equilibrium pair, the host never abandons a single nestling and the brood parasite always kills host young. This matches the behaviors shown by the reed warbler and the common cuckoo, respectively (Grim 2006b). Reed Warblers have never been observed to abandon single nestlings, even when broods of their own are manipulated to contain just one chick (Davies et al. 1998), and common cuckoos routinely evict host young. It is likely that this pair of strategies also describes the interactions of the common cuckoo and other hosts. It is not uncommon, for example, for dunnocks to raise single nestlings (Davies 1986). These strategies could also accurately describe other cuckoo and honeyguide species that routinely kill host nestlings (but see below for an exception).

It is harder to find examples to match the second pair of stable strategies identified by our model, in which the host always abandons single nestlings and the parasite does not kill host young, and our numerical analysis indicated that this should be by far the least common of the 3 strategy pairs predicted by the model. Among hosts of the more benign brood parasites, there is little indication that the absence of chick-killing has evolved in response to the threat of subsequent desertion by hosts. For example, magpie, *P. pica*, hosts continue to care for great spotted cuckoo, *C. glandarius*, young long after it has caused all their own chicks to starve to death (Soler JJ and Soler M 2000), and the same appears to be true of eastern phoebes, *Sayornis phoebe*, and other victims of the brown-headed cowbird (Hauber 2003a). Similarly, hosts of *Vidua* parasites willingly raise both single parasites and single host young (Payne et al. 2001; Schuetz 2005). Thus, there are numerous examples in which parasites do not kill host chicks and hosts do not abandon single nestlings, a situation that should never be an ESS according to our model. Perhaps in these host–parasite systems, the parasite has yet to select for changes in the host's life-history strategies (see below).

In the third stable equilibrium identified by our model, the likelihood that hosts will desert single chicks varies between 0 and 1, as does the propensity of cuckoos to kill host young. The behavior of the superb fairy-wren, *Malurus cyaneus*, the primary host of the Horsfield's bronze-cuckoo in south eastern Australia, is consistent with the model in that it abandons roughly 35% of all single nestlings it is given, whether they are Horsfield's bronze-cuckoos or single host chicks (Langmore et al. 2003). There is considerable variation among host females in their inclination to desert the nest (Langmore et al. 2003), but the Horsfield's Bronze-cuckoo nestling, by contrast, consistently evicts host young within 48 h of hatching (Payne RB and Payne LL 1998). Although the behavioral data superficially resemble an equilibrium predicted by the model, other explanations are possible. For example, perhaps nestling desertion is a coevolved strategy of defence against parasitism, driven by recognition of foreign offspring rather than a pre-existing life-history strategy in the host.

It might be argued that the deaths of host chicks that result from the presence of a brood parasite in the nest, but which do not result from chick-killing directly, also match the conditions for this equilibrium. Several of the more benign brood parasites are known to contribute to causing host nestling mortality, even though they have no means of evicting or killing young directly. Instead, their competitive superiority (e.g., Redondo 1993; Soler et al. 1995; Lichtenstein and Sealy 1998) deprives the host young of food and results in their death through starvation. In these instances, known in detail for the brown-headed cowbird and the great spotted cuckoo, at least, hosts routinely accept single offspring, but the chance that host young will die varies between 0 and 1. The predictions of our model suggest the possibility that in addition to choosing not to kill nest mates directly, parasites might sometimes adopt a "prudent" strategy of not monopolizing food to the point of starving all the nest mates.

In this paper, we effectively assume that occurrences of parasitism (*P*) and chick loss through other processes (*E*) are sufficiently small that the possibility of both occurring simultaneously can be ignored. If this is not the case, the same modeling system can still be used, but then the order of these events is important; if both occur and parasitism happens second, then the parasite will survive, whereas if it happens first, then it may not. To tackle such a system, one would need to consider a more detailed and flexible distribution of egg survival after natural destruction. We decided for reasons of simplicity to ignore such effects in this paper. However, it is likely that the predictions that we make will hold for higher values of *E* and *P* as all parasites will be affected by this irrespective of strategy, and we can get a good approximate model of the system by considering "effective" levels of parasitism and natural destruction adjusting for events up to the point that strategic choices are made (e.g., the effective level of parasitism would be the proportion of nests with surviving parasites). Another potential complication is that, for larger values of *P*, there is a nonnegligible probability of 2 (or more) parasites occurring in a single nest, and then the actions of the competing parasites are again more complex, and the strategies played will affect different individuals differently. Thus, the model is more sensitive to high values of *P* than it is to high values of *E*. The predictions are only likely to go seriously wrong for parasitism levels much higher than the conservatively chosen 0.15, however.

Another implicit assumption of our current model is that individuals targeted by brood parasites in 1 year are no more likely than other individuals to be targeted in future years (Hauber et al. 2004). If this is untrue, as it may well be in some systems, then this would make nest desertion a less attractive option to hosts than our current model predicts because the value of future nesting attempts will be relatively decreased. There may also be systems in which parasites kill only some of the host's offspring. Such an occurrence would not invalidate the results considered here but would enhance selection pressure for chick discrimination by the host adult. Similarly, if survival between reproductive attempts declined with age, one would expect older individuals to be less willing to desert their current nest.

There is an interesting asymmetry in the type of game between host and parasite explored in our model, in that all parasites experience a host but not all hosts experience a parasite (a rare enemy effect, sensu Dawkins and Krebs 1979). Thus, the strategic choice of behavior by the host has more influence on the reward to the parasite, than the choice of behavior by the parasite has on the reward to the host. Solutions involve the parasite getting the optimal strategic interaction between host and parasite. Consider a single interaction if a parasite is present, not taking into account future rewards. If the parasite's strategy is known, the optimal strategy for the host is to desert if the parasite kills host young and not to desert if it does not. On the other hand, the optimal strategy for a parasite, if the host's strategy is known, is to kill host young if the host will not desert and not to kill if it will desert. When future rewards are taken into account by the host, the 2 pure solutions are "eject and not desert" or "not eject and desert," which are again favorable to the parasite and not to the host. Thus, parasites will tend to do better in a host population where they have low penetration, for example, if they have many potential hosts. Of course, evolution works at the level of the individual so that such a situation may not be selected for even if it is the "group" interest. For example, if there is just one potential host, the population of parasites will evolve with the population of hosts, perhaps to some stable level where penetration is high.

Finally, just as in previous work (e.g., Soler 2002; Lyon and Eadie 2004), a key feature of the model presented here is that host responses to the brood parasitic young depend on the host's life history. But host life-history strategies might themselves evolve in response to parasitism. Previous work has shown that host clutch sizes evolve in response to exploitation by brood parasites (e.g., Lyon 1998; Soler JJ and Soler M 2000; Soler et al. 2001; Hauber 2003b), so other life-history traits might similarly be affected. It is possible, for example, that hosts might evolve a life-history strategy that favors the abandonment of single young after a prolonged history of interaction with a chick-killing brood parasite. According to our model, an increase in *B* by hosts will then favor the evolution of single chick desertion.

This raises the possibility of an intriguing dichotomy in the way that coevolution has shaped host responses to brood parasites. It could be that those exploited by chick-killing parasites mount defences involving recognition and rejection (Davies 2000), whereas those exploited by the more benign brood parasites have altered their life-history strategies (Lyon 1998; Soler JJ and Soler M 2000; Soler et al. 2001; Hauber 2003b). The conventional view is that the degree of virulence shown by the brood parasite is responsible for the contrast in host response. Our model suggests that the causal arrow can be reversed: perhaps a change in host life-history strategies can cause a virulent brood parasite to become more benign.

APPENDIX A

The relationship between the 5 conditions A–E and Figure 1

The 7 cases in Figure 1 are determined by their relationships to the roots of Equation 16. In (i), there is no such root occurring if $G_1^2 < 4G_0G_2$ (condition A^{C}). All other cases require A to occur with $G_1^2 > 4G_0G_2$, when there are 2 real roots. Case (ii) requires both roots larger than 1, so that

$$R_s = \frac{-G_1 + \sqrt{G_1^2 - 4G_0G_2}}{2G_2} > 1 \Rightarrow \sqrt{G_1^2 - 4G_0G_2} < 2G_2 + G_1. \tag{A1}$$

In conjunction with condition A, this equates to $2G_2 + G_1 > 0$ (condition D) and $G_1^2 - 4G_0G_2 < (2G_2 + G_1)^2 \Rightarrow G_0 + G_1 + G_2 < 0$ (condition E^{C}).

Given that $G_2 < 0$, these also imply $G_1 > 0$ (condition C) and $G_0 < 0$ (condition B^{C}).

Similar inequalities between either R_l or R_s and either 0 or 1 were used to establish the other conditions. In fact, there is a natural meaning to each of the 5 conditions, which makes it easy to see which corresponds to which case. A is the condition for the quadratic equation to have real roots, B is the condition that the value of this quadratic function at 0 is positive, that is, $f(0) > 0$, C is the condition that the slope of the function at 0 is positive ($f'(0) > 0$), D is the condition that this slope is positive at 1, that is, $f'(1) > 0$, and E is the condition that $f(1) > 0$. So, for example, from Figure 1 case (ii), we can see that neither B nor E occur but both C and D do.

Case (iii) requires both roots be <0. Case (iv) requires the larger root be >1 and the smaller root <0. For case (v), we need the larger root between 0 and 1 and the smaller root <0. Case (vi) requires the smaller root to be between 0 and 1 and the larger root >1. Finally, case (vii) requires both roots to be between 0 and 1.

The full breakdown of Figure 1 in relation to the 4 other conditions is, thus, as follows (remembering that case (i) is A "No," and all other cases require A "Yes"). Case (iv) B and E "Yes"; case (v) B "Yes," E "No"; case (vi) B "No," E "Yes." All other cases involve B and E "No." In addition, they need (ii) C and D "Yes"; (iii) C and D "No"; (vii) C "Yes" and D "No."

APPENDIX B

Stability of intermediate solutions where $0 < C_p^* < 1$

Suppose that we have a population almost entirely composed of individuals playing the equilibrium strategies (C_p^*, C_h^*), but we have a small fraction (x) of mutant parasites playing a different strategy (C_p), and a small fraction (y) of mutant hosts playing a different strategy (C_h). We need to consider the rewards to hosts and parasites in mixed populations and so must extend our previous notation. The reward to a host playing strategy C_h in the above mixed population can be written $R(C_h; xC_p, (1-x)C_p^*)$ and the reward to a parasite playing C_p in this population can be written $S(C_p; yC_h, (1-y)C_h^*)$. In fact, in the following working, all populations are of the above form, with 2 strategy types present in both hosts and mutants, and for simplicity, we will just write $R(C_h)$ for $R(C_h; xC_p, (1-x)C_p^*)$ and $S(C_p)$ for $S(C_p; yC_h, (1-y)C_h^*)$ in all of the following. The equilibrium will certainly be unstable if we can find a pair of mutant strategies where both $R(C_h) > R(C_h^*)$ and $S(C_p) > S(C_p^*)$.

In this case, we have $C_h^* = 1 - \phi$, and any parasite faces a host using strategies C_h and C_h^* with probabilities y and $1 - y$, respectively. Using this, it is easy to show that

$$S(C_p) - S(C_p^*) = (C_p^* - C_p)(C_h - C_h^*)y. \tag{A2}$$

Hence, the parasite mutants do better than the resident individuals if

$$(C_p^* - C_p)(C_h - C_h^*) > 0. \tag{A3}$$

To consider the host mutants, we can use the relation that intermediate equilibria can only occur if $\beta\gamma - \alpha\delta = 0$. That is, solutions of the form $(0 < C_p^* < 1; C_h^* = 1 - \phi)$ can only occur at the roots of

$$G_0 + G_1 C_p^* + G_2 (C_p^*)^2 = 0. \tag{A4}$$

In such a population, the payoff to an individual of the main population is

$$\begin{aligned} R(C_h^*) = {} & [(1-P-E)B + PcB + E - PcB(xC_p + (1-x)C_p^*) - EC_h^*]/ \\ & [1 - \mu_b + P(\mu_b - \mu_{bp}) + E(\mu_b - \mu_s) + EC_h^*(\mu_s - \mu_d) \\ & + P(xC_p + (1-x)C_p^*)((\mu_{bp} - \mu_p) + C_h^*(\mu_p - \mu_d))] \end{aligned} \tag{A5}$$

and the payoff to the mutants is

$$\begin{aligned} R(C_h) = {} & [(1-P-E)B + PcB + E - PcB(xC_p + (1-x)C_p^*) - EC_h]/ \\ & [1 - \mu_b + P(\mu_b - \mu_{bp}) + E(\mu_b - \mu_s) + EC_h(\mu_s - \mu_d) \\ & + P(xC_p + (1-x)C_p^*)((\mu_{bp} - \mu_p) + C_h(\mu_p - \mu_d))]. \end{aligned} \tag{A6}$$

With some algebra, we can show that

$$\begin{aligned} & R(C_h) - R(C_h^*) \propto -(C_p^* - C_p)(C_h - C_h^*)d_p(C_p^*)x - \\ & x^2(C_p^* - C_p)^2(C_h - C_h^*)P^2 cB(\mu_p - \mu_d), \end{aligned} \tag{A7}$$

where we define

$$d_p(C) = \frac{d}{dC_p}(G_2 C_p^2 + G_1 C_p + G_0)_{\text{at } C_p = C} = 2CG_2 + G_1. \tag{A8}$$

Ignoring small terms in x^2, we thus obtain $R(C_h) > R(C_h^*)$, providing

$$(C_p^* - C_p)(C_h - C_h^*)d_p(C_p^*) < 0. \tag{A9}$$

Thus, if $d_p(C_p^*) < 0$, then both parasite and host mutants do better if Equation A9 (and so Equation A2) is satisfied, and so the equilibrium is unstable. From the definition of $d_p(C_p^*)$, this means that any equilibrium where the function $f(x)$ is declining (with increasing x) when $f(x) = 0$, is unstable. This makes several of the equilibria identified in Table 1 unstable.

We now turn to the case where $d_p(C_p^*) > 0$. Under standard replicator dynamics, from Equations (A2) and (A9), we can describe changes in the frequencies of the mutants over time (t) by

$$\frac{\partial x}{\partial t} = xy\mathrm{k}_1(C_p^* - C_p)(C_h - C_h^*), \tag{A10}$$

$$\frac{\partial y}{\partial t} = -xyd_p(C_p^*)\mathrm{k}_2(C_p^* - C_p)(C_h - C_h^*) \tag{A11}$$

for positive constants k_1 and k_2. This means that for small mutant invasions either the mutant host or the mutant parasite will be eliminated but the other will persist (one of the 2 above derivatives is positive, the other negative for given mutant types). We can see from the above that

$$\frac{d}{dt}(d_p(C_p^*)\mathrm{k}_2 x + \mathrm{k}_1 y) = 0. \tag{A12}$$

If the mutant frequencies start at (x_0, y_0), then due to (A12), the end point of the evolution is either $(x_0 + \mathrm{k}_1 y_0 / d_p(C_p^*)\mathrm{k}_2, 0)$ or $(0, d_p(C_p^*)\mathrm{k}_2 x_0 / \mathrm{k}_1 + y_0)$. Thus, there is no evolutionary pressure for very small mutant groups. Subsequent mutations and/or drift may make the mutant proportion larger, but it will always finish with mutants of one type only.

What happens when there is a mutant proportion that is still small (but far larger than the initial mutation size) and a mutation of the other type occurs? If the proportion of host mutants has reached the larger value, then the population starts at (x_s, y_0) where x_s is small and thus finishes approximately at $(\mathrm{k}_1 y_0 / d_p(C_p^*)\mathrm{k}_2, 0)$ or $(0, y_0)$. There is either no change or a switch to this other mutant with the size of the mutant population as given above.

If the proportion of parasite mutants has reached the larger value, then the population starts at (x_0, y_s) where y_s is small. However, the differential equation for y has amended form because the initial average parasite strategy is $x_0 C_p + (1 - x_0)C_p^*$ so that

$$\frac{\partial y}{\partial t} = -xyd_{\mathrm{p}}(x_0 C_{\mathrm{p}} + (1 - x_0)C_{\mathrm{p}}^{*})\mathrm{k}_2(C_{\mathrm{p}}^{*} - C_{\mathrm{p}})(C_{\mathrm{h}} - C_{\mathrm{h}}^{*}) \tag{A13a}$$

if the above switch does not occur or

$$\frac{\partial y}{\partial t} \approx -xyd_{\mathrm{p}}(0.5x_0 C_{\mathrm{p}} + (1 - 0.5x_0)C_{\mathrm{p}}^{*})\mathrm{k}_2(C_{\mathrm{p}}^{*} - C_{\mathrm{p}})(C_{\mathrm{h}} - C_{\mathrm{h}}^{*}) \tag{A13b}$$

if the switch does occur, because we must consider the average parasite strategy as it moves from $x_0 C_{\mathrm{p}} + (1 - x_0)C_{\mathrm{p}}^{*}$ to C_{p}^{*} if the switch occurs, and the fixed value at $x_0 C_{\mathrm{p}} + (1 - x_0)C_{\mathrm{p}}^{*}$ otherwise. So the population finishes approximately at $(x_0, 0)$ or $(0, d_{\mathrm{p}}(0.5x_0 C_{\mathrm{p}} + (1 - 0.5x_0)C_{\mathrm{p}}^{*})\mathrm{k}_2 x_0/\mathrm{k}_1)$. There is either no change or a switch to this other mutant with the size of the mutant population as given above.

Suppose that parasite mutations increase or decrease the current value of their strategy C_{p} by a fixed amount a_{c}, and host mutations do the same with amount a_{h}. If different and multiple mutants are allowed, then the following analysis would be more complex, but not qualitatively different, provided that mutations of both host and parasite could occur in both directions. The key feature in showing stability is the average mutant strategy, and the simple form of function A8 indicates that stability should occur for various such mutation possibilities. Suppose further that the population starts at $(0, y_0)$. Mutations will either leave the population where it is, or move to $(\mathrm{k}_1 y_0/d_{\mathrm{p}}(0.5x_0 C_{\mathrm{p}} + (1 - 0.5x_0)C_{\mathrm{p}}^{*})\mathrm{k}_2, 0)$, so eventually this move will occur. Now mutations will either leave the population where it is or move it to

$$\begin{aligned}&(0, d_{\mathrm{p}}(0.5x_0 C_{\mathrm{p}} + (1 - 0.5x_0)C_{\mathrm{p}}^{*})(\mathrm{k}_2\mathrm{k}_1 y_0/d_{\mathrm{p}}(C_{\mathrm{p}}^{*})\mathrm{k}_2)/\mathrm{k}_1)\\ &\quad = (0, d_{\mathrm{p}}(0.5x_0 C_{\mathrm{p}} + (1 - 0.5x_0)C_{\mathrm{p}}^{*})y_0/d_{\mathrm{p}}(C_{\mathrm{p}}^{*})),\end{aligned} \tag{A14}$$

(where here $x_0 = \mathrm{k}_1 y_0/d_{\mathrm{p}}(C_{\mathrm{p}}^{*})\mathrm{k}_2$) which will thus eventually occur (but the host mutant value of C_{h} will be the other side of the equilibrium strategy). The next mutation must similarly eventually move the population to $(\mathrm{k}_1 y_0 d_{\mathrm{p}}(0.5x_0 C_{\mathrm{p}} + (1 - 0.5x_0)C_{\mathrm{p}}^{*})/d_{\mathrm{p}}^{2}\mathrm{k}_2, 0)$ (but the parasite mutant strategy will be the other side of the equilibrium, at $2C_{\mathrm{p}}^{*} - C_{\mathrm{p}}$). The next move returns the population to the same mutant mix as at the start but with a new frequency

$$\begin{aligned}&(0, d_{\mathrm{p}}(0.5x_0 C_{\mathrm{p}} + (1 - 0.5x_0)C_{\mathrm{p}}^{*})d_{\mathrm{p}}(-0.5x_0 C_{\mathrm{p}}\\ &\quad + (1 + 0.5x_0)C_{\mathrm{p}}^{*})y_0/d_{\mathrm{p}}^{2}(C_{\mathrm{p}}^{*})).\end{aligned} \tag{A15}$$

The population has moved closer to the equilibrium if and only if

$$\begin{aligned}&d_{\mathrm{p}}(0.5x_0 C_{\mathrm{p}} + (1 - 0.5x_0)C_{\mathrm{p}}^{*})d_{\mathrm{p}}(-0.5x_0 C_{\mathrm{p}}\\ &\quad + (1 + 0.5x_0)C_{\mathrm{p}}^{*})/d_{\mathrm{p}}^{2}(C_{\mathrm{p}}^{*}) < 1.\end{aligned} \tag{A16}$$

By substituting the result from A8, A16 reduces to

$$\begin{aligned}&\frac{(2G_2 C_{\mathrm{p}}^{*} + G_1 + x_0 G_2(C_{\mathrm{p}} - C_{\mathrm{p}}^{*}))(2G_2 C_{\mathrm{p}}^{*} + G_1 - x_0 G_2(C_{\mathrm{p}} - C_{\mathrm{p}}^{*}))}{(2G_2 C_{\mathrm{p}}^{*} + G_1)^2}\\ &\quad = 1 - \frac{(C_{\mathrm{p}} - C_{\mathrm{p}}^{*})^2 x_0^2 G_2^2}{(2G_2 C_{\mathrm{p}}^{*} + G_1)^2} < 1,\end{aligned} \tag{A17}$$

which is clearly true. We thus have the required result. There is pressure toward the equilibrium value once the mutant size becomes sufficiently large (but still small). This equilibrium can thus be considered stable, although small oscillations from this equilibrium will occur and persist for periods of time.

In summary, we can delineate those internal equilibria that are evolutionarily stable and those that are not.

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