



Retaliatory cuckoos and the evolution of host resistance to brood parasites

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We present a dynamic model of the evolution of host resistance to avian brood parasites, when the latter can retaliate against hosts that reject parasitic eggs. In a verbal model, Zahavi (1979, *American Naturalist*, 113, 157–159) suggested that retaliatory cuckoos might prevent the evolution of host resistance by reducing the reproductive success of rejecter hosts (i.e. by destroying their eggs or nestlings). Here we develop a model based on the association between the great spotted cuckoo, *Clamator glandarius*, and its main host, the European magpie, *Pica pica*, because this is the only system that has provided supportive evidence, to date, for the existence of retaliatory behaviour. Our aims were (1) to derive the conditions for invasion of the retaliation strategy in a nonretaliatory parasite population and (2) to investigate the consequences of retaliation for the evolution of host defence. If we assume a cost of discrimination for rejecter hosts in the absence of parasitism, and a cost paid by a retaliator for monitoring nests, our model shows cyclical dynamics. There is no evolutionarily stable strategy, and populations of both hosts and parasites will cycle indefinitely, the period of the cycles depending on mutation and/or migration rate. A stable polymorphism of acceptors and rejecters occurs only when parasites are nonretaliators. The spread of retaliator parasites drives rejecter hosts to extinction.

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Interspecific brood parasitism is a means of reproduction in which some individuals, the parasites, are reared by unrelated individuals belonging to another species, the hosts. This reproductive strategy can be extremely costly for hosts because the reproductive success of a parasitized host is usually dramatically reduced, sometimes with complete loss of a clutch (Rothstein 1990). The reduction of host reproductive success varies according to both host and parasite species. Some host species are able to discriminate parasitic eggs and either reject or abandon them (Rothstein 1990). In other species, acceptance of parasitic eggs is common (Rothstein 1990; Brooker & Brooker 1996). Because acceptance of cuckoo eggs generally lowers host reproductive success (even in the case where both host and cuckoo chicks are reared together), this behaviour appears to be maladaptive.

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Several hypotheses have been put forward to explain the coexistence of ejection and acceptance within a host population. The evolutionary lag hypothesis assumes that all hosts have not yet evolved the faculty to discriminate correctly against the parasite (Dawkins & Krebs 1979; Davies & Brooke 1988; Rothstein 1990). Alternatively, brood parasites and their hosts might have reached an evolutionary equilibrium (Lotem et al. 1991, 1995; Marchetti 1992). In this case, persistence of acceptance would be the result of an adaptive balance between costs (e.g. rejection errors) and benefits of host resistance (Lotem & Nakamura 1998).

Another type of cost for rejecter hosts could arise from the parasite itself, as suggested by Zahavi (1979). If the parasite revisits parasitized nests and preys upon nests where the parasitic egg has disappeared, the advantage for discriminating hosts is reduced or disappears. This retaliatory or 'Mafia' behaviour by parasites could thus prevent the fixation of the rejection strategy in a host population. Recently, Pagel et al. (1998) developed a theoretical model of retaliatory behaviour by cuckoos and investigated how retaliation affects host strategies of rejecting versus accepting the cuckoo chicks. They showed that, in

Table 1. Definition of parameters used in the models

Parameters	Definition	Values
Concerning the parasite		
x	Probability of a retaliatory cuckoo detecting ejection and destroying the nest	Unknown
δ	Cost paid by retaliator for monitoring nests	Unknown
s_{1p}	Adult survival	Fixed
s_{0p}	Juvenile survival	Fixed
Concerning the host		
n	Average fecundity when nest not parasitized	Fixed
c_p	Cost of rearing a cuckoo	Fixed
c_r	Cost of rejection	Unknown
c_d	Cost of discrimination	Unknown
w	Cost of laying late in reproductive season	Fixed
s_0	1-year-old intrinsic survival rate	Fixed
s	Adult intrinsic survival rate	Fixed
β	Coefficient of survival density	Fixed
v	Fecundity reduction for yearlings	Fixed

the presence of a retaliatory cuckoo, rejection of the cuckoo's young by hosts was indeed selected against. Significantly, these authors showed that acceptance and rearing of the cuckoo's chicks can evolve even in the extreme case in which the cuckoo chick ejects all of the host's clutch from the nest, and thus hosts pay very high costs. A key condition for such evolution is that acceptors enjoy lower rates of parasitism in later clutches, compared to rejectors.

Here we present a quantitative theoretical model that is specific to a well-studied system, that of the great spotted cuckoo, *Clamator glandarius*, and its European magpie, *Pica pica*, hosts. This is the only system where retaliation against rejecter hosts has been shown experimentally (Soler et al. 1995). We built a population dynamic model in which both host (i.e. the magpie) and parasite (the great spotted cuckoo) interact over many breeding seasons. In particular, we (1) derive the conditions for invasion of the retaliation strategy in a nonretaliatory parasite population and (2) investigate the consequences of retaliation for the evolution of host defence.

THE MODEL

We consider four possible strategies: two for the parasite and two for the host. A retaliatory parasite revisits nests that it has parasitized and, if its egg has been removed, destroys the host clutch with a probability x ($0 < x < 1$) (see Table 1). In contrast, a nonretaliatory parasite does not monitor the parasitized nest. When parasitized, a host can be either a rejecter or an acceptor. We explored all the possibilities by introducing successive mutants into populations of hosts and parasites. We started with a naïve host population exploited by nonretaliatory parasites. At equilibrium, we introduced a mutant rejecter host, and then a retaliator parasite.

Fecundity is here defined as the number of fledglings per clutch per female. Each female has one brood per year; when this clutch fails there is always a replacement clutch. If the replacement clutch fails, the female's reproductive success is nil for this year. Let n be the fecundity of acceptor hosts in a nonparasitized first clutch. When the first clutch is parasitized, an acceptor female will fledge only $n(1 - c_p)$ young, where c_p represents the cost of being parasitized (i.e. the reduction in reproductive success due to the parasite). Great spotted cuckoos do not eject the magpies' eggs, but even so, Soler et al. (1995) estimated that the fitness of a parasitized magpie nest can be reduced by 0.7 (where 1.0 is the maximum).

If the first clutch fails, the female will rear $n(1 - w)$ chicks in a replacement clutch. The parameter w indicates the cost of laying later in the reproductive season. For rejecter hosts fecundity is $n(1 - c_r)$ when they are parasitized and reject the parasite egg, where c_r is the cost of rejection (i.e. the probability that a host damages its own eggs when rejecting the cuckoo egg). We also assume that there is a discrimination cost paid by rejecters in the absence of parasitism (when hosts mistakenly reject one of their own eggs). When not parasitized, a rejecter will rear an average of $n(1 - c_d)$ young. All costs are multiplicative, thus a rejecter whose first clutch is destroyed by a retaliatory cuckoo will rear $n(1 - w)(1 - c_d)$ young.

Hosts can adopt two strategies: they can accept the parasitic egg or reject it (a and r being the rates of each strategy among hosts). All hosts and parasites are supposed to maintain the same strategy throughout their life. We assume that host antiparasite behaviour and the cuckoo's retaliation behaviour are determined by genetic factors (Rothstein 1990; Takasu et al. 1993). Each female magpie and cuckoo inherits its mother's strategy.

For specialist brood parasites, which exploit only one host species, it is plausible to assume that the parasite population depends directly on the density of the host population (May & Robinson 1985). The relationship between the number of parasites $P(t)$ and the number of hosts $H(t)$ is given by the probability $p(t)$ of parasitism for a given host nest. The laying period of magpies extends from early April to June, and as the breeding season proceeds, the frequency of parasitism tends to increase (Soler 1990; Martinez et al. 1996), probably because nest availability decreases as the season progresses. We therefore considered in our model that replacement clutches have a higher probability of being parasitized than first clutches.

The probability that a host nest escapes parasitism is given by the zero term of a Poisson distribution (May & Robinson 1985) as

$$1 - p(t) = e^{-\alpha P(t)}, \quad (1)$$

α being the searching efficiency of the parasite. We considered α as depending on available host nests (Thomson 1924) so that

$$\alpha(t) = \frac{k}{H(t)} \quad (2)$$

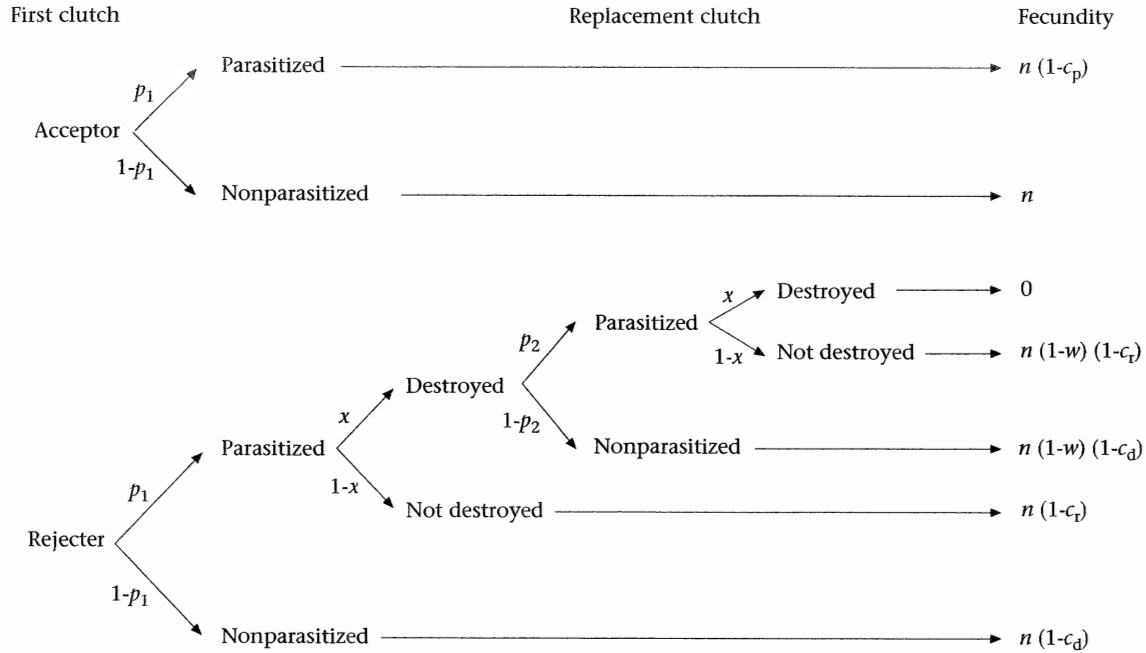


Figure 1. Possible outcomes for a host playing either the acceptor or rejecter strategy when parasites are retaliators. For parameter definitions see Table 1.

where k indicates the average number of eggs that a cuckoo can lay during a reproductive season.

To obtain the probability of being parasitized by nonretaliators (p_1), we replaced α in equation (1)

$$p_1(t) = 1 - e^{-k(P_R(t)/H(t))} \quad (3)$$

where $H(t)$ is the number of host females in nonretaliator territories.

Assuming there is a cost for monitoring nests, retaliator cuckoos lay fewer eggs than nonretaliators. Let p'_1 and p'_2 be the probabilities of being parasitized in first and replacement clutches for hosts of a retaliator parasite. We assumed that

$$p'_1(t) = (1 - \delta)(1 - e^{-k(P_R(t)/H'(t))}) \quad (4)$$

$$p'_2(t) = 1 - e^{-k(P_R(t)/H'_{2c}(t))} \quad (5)$$

where δ is the cost of retaliation, $P_R(t)$ represents the number of retaliator parasites, $H'(t)$ the number of female hosts in retaliator territories and $H'_{2c}(t)$ the number of replacement clutches at time t in retaliator territories.

$$H'_{2c}(t) = p'_1(t)H'(t)r'(t)x \quad (6)$$

where $r'(t)$ is the rejection rate in retaliator territories. We supposed that all females breed. Only parasitized rejecter females will have their nest destroyed by retaliatory cuckoos and then they will lay a replacement clutch.

Dynamics of the Host Population

The dynamics of each host strategy can now be described by the annual fecundity and survival rates

associated with each strategy, depending on the presence of retaliatory or nonretaliatory parasites. We divided the host population into two age classes: yearlings and older birds (more than 1 year old). The fecundity of yearlings (f_0) was considered to be lower than adult fecundity (f) (Birkhead 1991), i.e. $f_0 = f(1 - \nu)$, where ν is the reduction in fecundity.

The equations for adult annual fecundity in the territory of a nonretaliatory parasite are:

$$f_A(t) = p_1(t)(1 - c_p)n + (1 - p_1(t))n \quad (7)$$

for acceptor hosts, and

$$f_R(t) = p_1(t)(1 - c_r)n + (1 - p_1(t))n(1 - c_d) \quad (8)$$

for rejecter hosts.

The equations for adult annual fecundity in a territory of a retaliatory parasite are (Fig. 1):

$$f'_A(t) = p'_1(t)(1 - c_p)n + (1 - p'_1(t))n \quad (9)$$

$$f'_R(t) = (1 - p'_1(t))n(1 - c_d) + p'_1(t)(1 - x)n(1 - c_r) + p'_1(t)x(1 - p'_2(t))n(1 - w)(1 - c_d) + p'_1(t)xp'_2(t)(1 - x)n(1 - w)(1 - c_r). \quad (10)$$

Usually, fledgling survival rate is considered as being independent of whether it comes from parasitized or nonparasitized nests. However, this assumption might be incorrect. Magpie fledglings from parasitized nests weigh less than those from nonparasitized clutches (Soler & Soler 1991). Given that postfledging survival is positively correlated with body mass in magpies (Birkhead 1991), it is plausible to expect lower juvenile survival rate for host

young fledged from parasitized nests (see also Payne & Payne 1998). We assumed, then, that host survival rate is negatively correlated with the number of young fledged (Birkhead 1991), and juvenile survival is negatively affected by parasitism. The trade-off between survival and reproduction was described by a linear function (van Noordwijk & de Jong 1986). We also assumed that the survival cost of rearing a cuckoo nestling is equivalent to the survival cost of rearing a magpie chick, since they have similar sizes.

Finally, we assumed that survival rate is density dependent, to take into account the fact that, in the absence of parasitism, host density is regulated by the availability of food and territories (Birkhead 1991). We chose a simple density-dependent function. If $s_0(t)$ is the survival rate of 1-year-old hosts and $s(t)$ the survival of older hosts, we have

$$s_0(t) = \frac{s_0}{1 + \beta H_T(t)} \quad \text{and} \quad s(t) = \frac{s}{1 + \beta H_T(t)} \quad (11)$$

where β is the coefficient of density dependence, s_0 and s are the intrinsic survival rates when food and territories are unlimited for 1-year-old and older individuals, respectively and $H_T(t)$ is the total number of hosts ($H'(t) + H(t)$).

Annual fecundities and survival were then used to compute host population size at time $t+1$ for each strategy and each age class of hosts as a function of the number of hosts at time t . The number of nonrejecter host females in nonretaliator territories ($H_{AO}(t)$ and $H_{A1}(t)$, where $H_{AO}(t)$ is the number of 1-year-old acceptor females and $H_{A1}(t)$ is the number of older acceptor females) is derived as follows:

$$Z_A(t+1) = \begin{bmatrix} 0.5f_{AO}(t)s_0(t) & 0.5f_A(t)s(t) \\ s_0(t) & s(t) \end{bmatrix} Z_A(t) \quad (12)$$

where

$$Z_A(t) = \begin{bmatrix} H_{AO}(t) \\ H_{A1}(t) \end{bmatrix},$$

$s_0(t)$ and $s(t)$ are 1 year old and adult survival rates, respectively (as given in equation 11), and $f_A(t)$ and $f_R(t)$ are given in equations (7) and (8) for nonretaliator parasites. We have $f_{AO}(t) = f_A(t)(1 - \nu)$ and $f_{BO}(t) = f_B(t)(1 - \nu)$.

Similarly, we calculated $H_{RO}(t)$ and $H_{R1}(t)$, the number of rejecter hosts in nonretaliator territories, and the number of acceptors in retaliator territories ($H'_{AO}(t)$ and $H'_{A1}(t)$), where $f_A(t)$ and $f_R(t)$ are replaced by $f'_A(t)$ and $f'_R(t)$ (given in equations 9 and 10).

The total number of hosts, $H_T(t)$, is defined as

$$H_T(t) = H_{AO}(t) + H_{A1}(t) + H_{RO}(t) + H_{R1}(t) + H'_{AO}(t) + H'_{A1}(t) + H'_{RO}(t) + H'_{R1}(t). \quad (13)$$

The acceptor rate at time (t) in nonretaliator territories is

$$a(t) = \frac{H_A(t)}{H_R(t) + H_A(t)} \quad (14)$$

where $H_R(t) = H_{R1}(t) + H_{RO}(t)$ and $H_A(t) = H_{A1}(t) + H_{AO}(t)$. Identically, the acceptor rate at time (t) in retaliator territories $a'(t)$ is

$$a'(t) = \frac{H'_A(t)}{H'_R(t) + H'_A(t)} \quad (15)$$

where $H'_R(t) = H'_{R1}(t) + H'_{RO}(t)$ and $H'_A(t) = H'_{A1}(t) + H'_{AO}(t)$. The global rate of acceptor ($a_g(t)$) in the whole population of hosts is given by

$$a_g(t) = \frac{H_A(t) + H'_A(t)}{H_T(t)}. \quad (16)$$

Dynamics of the Parasite Population

We assumed an even sex ratio (1:1), and that cuckoo juveniles are recruited into the local population when they are 1 year old. We considered only one age class for the parasite. Cuckoos produce fledglings only in nests of acceptor hosts. The equation relating the number of female adult parasites in successive years is then

$$P(t+1) = s_{1p}(t)P(t) + 0.5 s_{op}(t)p_1(t)H(t)a(t) \quad (17)$$

where the first term of the right side represents the number of adult female survivors and the second term represents the newly recruited yearlings. Here s_{1p} and s_{op} are the probabilities of adult and juvenile survival of the parasite. We also assumed that survival probability of the parasite does not depend on host antiparasite behaviour.

Identically, the equation relating the number of retaliator adult parasites in successive years is

$$P_R(t+1) = s_{1p}(t)P_R(t) + 0.5 s_{op}(t)p'_1(t)H'(t)a'(t). \quad (18)$$

We assumed that parasites defend territories. The size of the territories is related to the number of host nests, each cuckoo having at least 20 host nests in its territory (Cramp 1985). Each year, some hosts migrate from retaliator territories to nonretaliator territories so that each territory has the same number of hosts. For instance, if nonretaliatory parasites exploit $H(t)$ hosts in their territories (with an acceptor rate of $a(t)$) and retaliatory parasites exploit $H'(t)$ hosts (with an acceptor rate of $a'(t)$) after the host's reproduction, and if $H(t)$ is higher than $H'(t)$, then $(H(t) - H'(t))/2$ hosts will migrate from non-retaliator territories to retaliator ones, in such a way that there is the same number of hosts at the beginning of each reproductive season in retaliator and nonretaliator territories. In this case, the proportion of acceptor hosts among migrants is $a(t)$. The number of hosts that a cuckoo can exploit is defined by the total number of hosts divided by the total number of parasites. When the number of cuckoos exceeds the number of available territories, we assumed that some cuckoos migrate to other host populations.

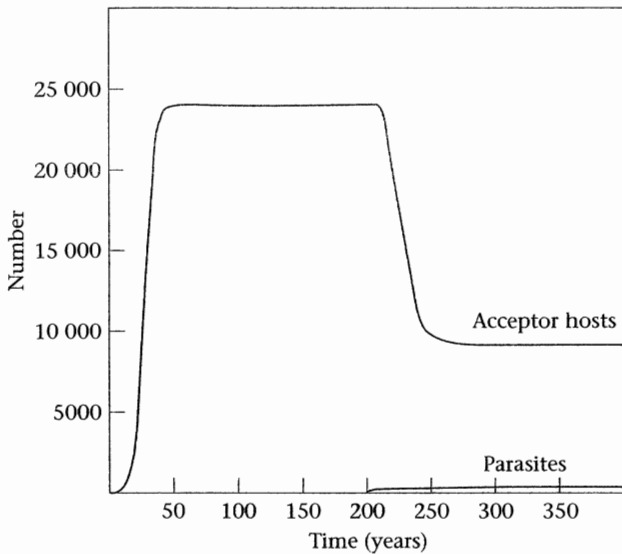


Figure 2. Change in number of hosts after introduction of a nonretaliatory parasite (at time $t=200$). Parameter values are: $n=3.5$, $w=0.15$, $c_p=0.7$, $c_r=0.1$, $s_{1p}=0.7$, $s_{0p}=0.3$, $\beta=10^{-5}$, $s=0.8$, $s_0=0.4$, $v=0.4$. For parameter definitions see Table 1.

Numerical simulations were run using the population dynamics software ULM (Legendre & Clobert 1995).

RESULTS

In the first step of the model we considered a population of acceptor hosts and derived the population size at equilibrium (which depends on the value of the density dependence coefficient). Introduction of a nonretaliatory female cuckoo produced the convergence of both populations (host and parasite populations) to new equilibrium values (Fig. 2). We then tested if the rejecter strategy could invade an acceptor host population in the presence of a nonretaliatory parasite. As expected, the rejecter strategy rapidly spreads among hosts (Pagel et al. 1998). Both rejecters and acceptors coexist at equilibrium because of the cost of discrimination paid by rejecters when not parasitized (Fig. 3).

Introduction of a rejection strategy leads to a decrease in parasitism rate, and the frequencies of both rejecters and parasites exhibit damped oscillations, converging to the equilibrium state (Fig. 3). In the absence of costs of discrimination, rejecters invade the acceptor population, and the parasite population goes extinct (Fig. 4). When we assume a discrimination cost, the proportion of acceptors is sufficiently large to allow the parasite population to survive. The proportion of acceptors is determined by the intensity of discrimination costs; variable levels of the cost of discrimination produce different equilibrium values of rejecters (Fig. 5). Rejector frequency is unity when there is no discrimination cost; it decreases slowly when the discrimination cost increases, and after a certain value of discrimination cost (around 0.75) rejection frequency rapidly declines (Fig. 5).

In a second step, we considered a population of rejecter and acceptor hosts exploited by a nonretaliator

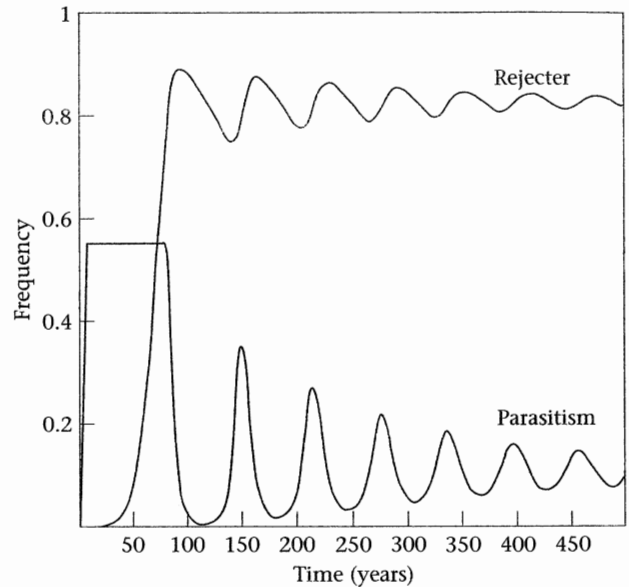


Figure 3. Change in parasitism rate and rejecter frequency after introduction of a rejecter host at time $t=0$. Parameters used are: $c_d=0.1$, $c_r=0.1$. Other parameter values as in Fig. 2. For parameter definitions see Table 1.

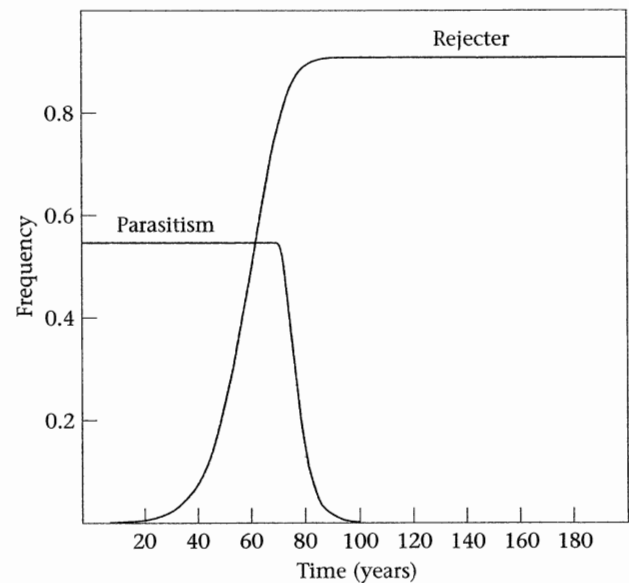


Figure 4. Change of rejecter frequency and parasitism rate after introduction of a host rejecter mutant at time $t=0$ for $c_d=0$. Other parameter values as in Fig. 2. For parameter definitions see Table 1.

population of parasites at equilibrium and we introduced a retaliatory mutant. Similar to Pagel et al.'s (1998) results, the conditions for a retaliatory mutant to invade a nonretaliatory parasite population depend on the retaliation (monitoring) cost (δ) and the level of retaliation (χ) (Fig. 6). The higher the retaliation cost, the higher the level of retaliation has to be to allow retaliation to spread. If there is no cost of retaliation, then the minimum value of retaliation required for invasion is around 10%. For retaliation costs larger than 45% (e.g. 45% reduction in

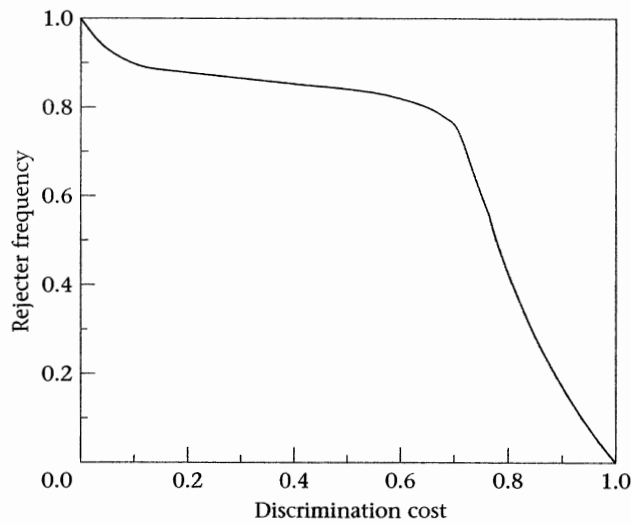


Figure 5. Rejection frequency at equilibrium as a function of discrimination cost. Parameter values as in Fig. 2. For parameter definitions see Table 1.

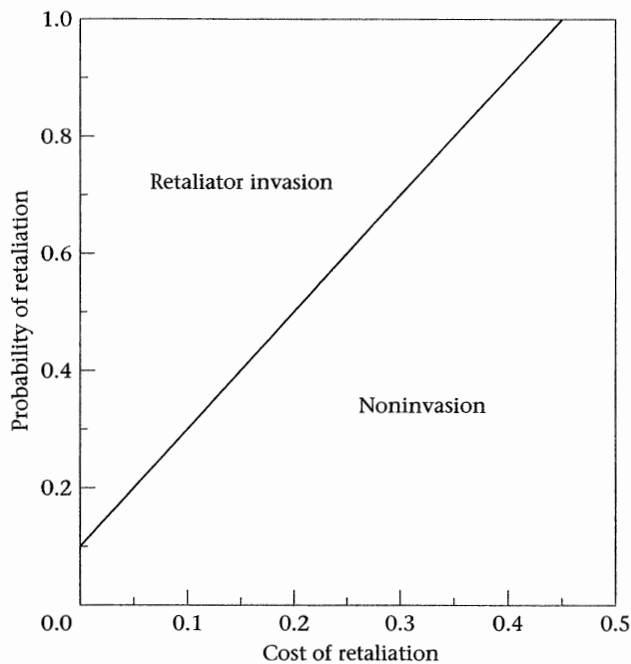


Figure 6. Conditions for the invasion of retaliation in a nonretaliatory parasite population as a function of the probability of retaliation (x) and the cost of retaliation (δ). Other parameter values as in Fig. 3. For parameter definitions see Table 1.

fecundity of retaliatory parasites), retaliation cannot invade, even when retaliation is maximal (100%).

When conditions for invasion are met, retaliation strongly selects for acceptor hosts, resulting in the extinction of rejecter hosts (Fig. 7). At equilibrium, only retaliator parasites and acceptor hosts coexist. Acceptor rate corresponds to the global rate of the whole host population. Therefore, acceptor strategy has a selective advantage in the presence of retaliatory parasites.

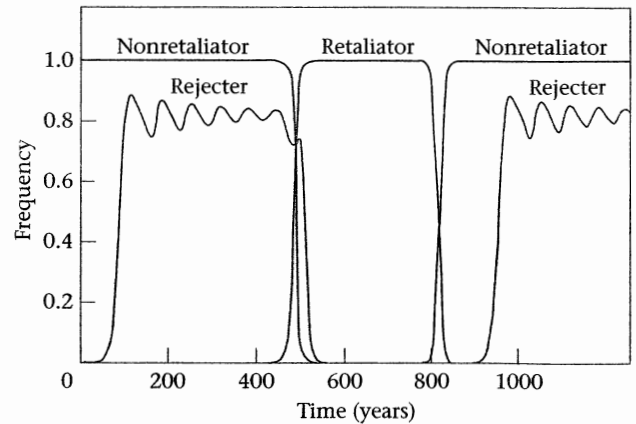


Figure 7. Frequency of rejecter hosts, retaliatory parasites and nonretaliatory parasites as a function of time. At time $t=0$, a rejecter mutant arrives in an acceptor host population exploited by nonretaliatory parasites at equilibrium. At time $t=400$, we introduce a retaliator parasite. At time $t=790$, we introduce a nonretaliator parasite. At time $t=900$, a rejecter mutant is introduced.

In the final step, we considered whether nonretaliation could beat retaliation given that the host population now contains only acceptor hosts. As expected, nonretaliatory parasites rapidly spread into the parasite population, reaching the same equilibrium as for the initial populations (Fig. 7).

DISCUSSION

Why should passerine species accept and take care of parasitic eggs and nestlings? Zahavi (1979) proposed a verbal argument to explain the persistence of acceptance behaviour in host species, despite a high cost of parasitism. According to Zahavi, brood parasites might reduce or even nullify the benefits of resistance by depreeding nests of rejecter hosts, preventing the fixation of rejecter genes in the host population. Pagel et al. (1998) have confirmed the plausibility of this conjecture in their theoretical model, and anecdotal evidence supports the idea that brood parasites might also act as nest predators. Soler et al. (1995) have additionally provided experimental evidence for retaliatory behaviour in great spotted cuckoos parasitizing magpie nests.

In this study we allowed the different strategies of both hosts and parasites to compete over long periods of time, incorporating the survival probabilities of both hosts and parasites. The results show that host resistance (i.e. rejection) and parasite virulence (i.e. retaliation) could evolve following a cyclic pattern, where virulence is selected for as long as host resistance increases and is selected against as long as host susceptibility increases (Fig. 7).

Evolution of Retaliation

Zahavi's idea that brood parasites can act as nest predators to prevent the spread of rejecter genes was initially criticized by Guilford & Read (1989). They argued that retaliation cannot confer any selective advantage to

a retaliatory parasite since punishment occurs when the reproductive success of the parasite is already nil (i.e. the host has ejected the parasite egg). Benefits of retaliation can, however, arise from two distinct phenomena. First, if retaliation induces the host to relay, the parasite can gain from further breeding opportunities (Soler et al. 1995, in press; Pagel et al. 1998). Second, retaliation can be selected for if it decreases the local host rejection rate, and this benefits the retaliatory cuckoo or its kin. This latter phenomenon remains to be analysed.

The results of our model indicate that retaliation actually selects against host resistance and that the increase in acceptance rate can be sufficiently rapid to allow this strategy to invade a nonretaliatory parasite population. However, retaliation invades only in a limited part of parameter space. The conditions for invasion mostly depend on the cost and level of retaliation. Using parameter values estimated from experimental evidence of retaliation in the great spotted cuckoo (Soler et al. 1995), our model shows that retaliatory cuckoos eliminate nonretaliatory ones. Interestingly, at equilibrium, all parasites are retaliators and all hosts are acceptors. Retaliation can invade a nonretaliator population of parasites, but it can also be invaded by nonretaliators once all hosts become acceptors. If we assume no cost of retaliation, then retaliation becomes an evolutionarily stable strategy (ESS), and can no longer be invaded by nonretaliation.

Evolution of Host Resistance

When parasites are nonretaliators, the introduction of a rejecter host leads to a stable polymorphism within the host population. However, rejection remains the dominant strategy even for quite high costs of discrimination (costs paid in the absence of parasitism).

A cost of discrimination is a sufficient condition to explain the persistence of acceptor hosts and therefore the persistence of the parasite at equilibrium. Retaliation never leads to a stable polymorphism in the host population. Rejecters and acceptors coexist only during a transition period. Therefore, contrary to Zahavi's (1979) hypothesis, our model suggests that retaliation would not account for the observed polymorphism in resistance within a host population; however, if a retaliator mutant appears, it will spread rapidly in the parasite population. After invasion of retaliation, rejecter hosts go extinct, although the possibility of coexistence between retaliators and rejecters when egg discrimination is not perfect should be explored in future models.

Rejecter hosts can pay two types of costs. In the presence of parasitism they can damage one or more of their own eggs when handling parasitic eggs (rejection costs) (e.g. Sealy 1996). In the absence of parasitism they can mistakenly reject one of their own eggs as a cuckoo egg (discrimination costs; Marchetti 1992). In the absence of discrimination costs, rejecters and acceptors cannot coexist at equilibrium in our model; consequently when rejecters invade, cuckoos are driven to extinction.

Hosts of brood parasites can adopt a third strategy to reduce costs of parasitism: they can abandon parasitized

clutches (Rothstein 1990). Deserters pay a higher cost than rejecters when they are parasitized, because they always desert their nest, whereas rejecters have a probability x ($x < 1$) of having their nest destroyed. Furthermore, both phenotypes have the same probability of being parasitized in replacement clutches. As a consequence, desertion is unlikely to be the best strategy available for hosts. Data on magpies parasitized by the great spotted cuckoo show that desertion is infrequent in this population (Soler et al. 1998).

One of the most crucial assumptions of our model is that late breeders have a higher probability of being parasitized than do early breeders. Here again our choice was based on empirical data showing that the probability of parasitism is negatively correlated with the number of host nests simultaneously available for the parasite (Martinez et al. 1996). Relaxing this assumption (or even assuming that late breeders have a lower probability of parasitism) would probably modify some of our conclusions. If we assume that first and replacement clutches have the same probability of being parasitized, then even for levels of retaliation close to one, retaliators can never spread in a nonretaliator population, the decrease in rejection frequency not being fast enough to balance the cost of retaliation. Actually, our simulations show that the difference in parasitism rate between first and replacement clutches should at least equal 0.4 to allow retaliation to invade. This critical threshold was calculated for parameter values as for Fig. 2.

We have shown that for both hosts and parasites, none of the strategies they can adopt is an ESS (for retaliation and discrimination costs higher than zero). Hence, when appropriate mutations occur (or when the rare genotype appears by migration), a new pair of strategies will be selected for until either mutation or migration again changes the equilibrium values. If this kind of cyclic behaviour, where susceptible and resistant hosts play against virulent and avirulent parasites, was a general rule of host-brood parasite interactions, it might prove extremely difficult to interpret the observed patterns of host resistance.

In conclusion, our model shows that a behavioural polymorphism (rejecter and acceptor) persists among hosts at equilibrium only when parasites are non-retaliators. Because of costs associated with each strategy, the model leads to cyclic population dynamics, where there is no ESS. Furthermore, selective pressures against egg discrimination, in the form of cost of ejection, seem to be the necessary condition allowing the coexistence of rejecter and acceptor within a host population.

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