Population dynamics and avian brood parasitism: persistence and invasions in a three-species system

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Summary

1. Avian brood parasites include species that are host specialists and others that are generalists. The impact of each kind of parasite on the persistence of the host population is studied by means of a population dynamics model.

2. Our model examines conditions for coexistence and invasions in a community of three South American cowbirds, the shiny cowbird *Molothrus bonariensis* (a generalist parasite), the screaming cowbird *M. rufoaxillaris* (a specialist parasite), and the bay-winged cowbird *Agelaiodes badius* (a nonparasite that hosts the other two).

3. Three biologically realistic characteristics not previously included in brood parasitism models are explored and shown to be crucial for the stability of the system. These characteristics are: (i) female parasites take at least a day to produce an egg and cannot store eggs for delayed laying – this is modelled by means of a type II functional response; (ii) parasites often remove or puncture (destroy) host eggs when visiting a nest; and (iii) hosts desert nests when the total clutch (host plus parasite) exceeds some threshold.

4. These characteristics have a direct impact on parasite population renewal and reduce dramatically the stable coexistence conditions.

5. Comparing the stability conditions of the host–specialist system with those of the three-species system shows the impact of the arrival of a generalist parasite on the persistence of the host–specialist system when the three characteristics are present. The stability boundaries are restricted when the generalist is absent and change little for a realistic density of generalist.

6. The study of invasion by a specialist into a host–generalist stable community shows that the parameter region for coexistence and invasion coincide.

7. Comparison of our model against its precursors using field data for the parameters when available, shows that the three-species cowbird model system is stable for empirically realized parameter values, unlike a previous model by May & Robinson (1985; *American Naturalist*, **126**, 475–494) where none of the three characteristics were included.

Key-words: brood parasitism, cowbirds, population dynamics, host specialism, *Molothrus* sp.

Introduction

Brood parasites include generalists that use a wide range of hosts, and specialists that use very few. Specialists

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are rarer both in species number and abundance within a species (Rothstein & Robinson 1998; Davies 2000). Here we present a study of the population dynamics of a system of three species of South American cowbirds, two brood parasites, and a host for the former two.

The existence of systems with more than one parasite attacking the same host raises problems for both ecological and evolutionary stability. If a specialist and a

generalist attack one host, it is of immediate interest to study whether one parasite may displace the other, or drive the host and hence the specialist to extinction. The ecological analysis may also throw light on the evolution path from generalism to specialization or vice versa.

Specialism at species level occurs in most African indigobirds (*Vidua* spp.) that parasitize different species of close relative grassfinches (Payne *et al.* 2000; Sorenson *et al.* 2003). Within a species, the common cuckoo *Cuculus canorus* is divided into host-specific races (gentes) that specialize in different hosts (Davies 2000). Females of each race lay a distinctive egg type that tends to match the host's egg. Gentes are restricted to female lineages, with cross-mating by males maintaining the common cuckoo genetically as one species (Gibbs *et al.* 2000). In the brown-headed cowbird *Molothrus alter* some females use more than one host species, both within and between breeding seasons, while other females parasitize specific host species regardless of their availability. This raises the possibility that brown-headed cowbird populations may consist of combinations of females some of whom are host generalists and others host specialists (Alderson, Gibbs & Sealy 1999; Woolfenden *et al.* 2003).

Brood parasitism poses a threat to some host populations (Robinson *et al.* 1995a,b; Trine, Robinson & Robinson 1998). Generalists are particularly threatening because their populations may be uncoupled from that of their relatively uncommon hosts. In contrast, specialists are less likely to drive hosts to extinction because their population dynamics are coupled to their host's (May & Robinson 1985; Takasu *et al.* 1993). The impact of generalist and specialist parasites depends on the characteristics of the system each forms with their hosts.

Although host–brood parasite systems have received less attention than host–parasite or host–parasitoid systems, several authors have examined the problem (May & Robinson 1985; Takasu *et al.* 1993; Haraguchi & Seno 1995; Grzybowski & Pease 1999; Woodworth 1999). Work on systems formed by a host, a generalist, and a specialist parasitoid has shown that the conditions for the persistence of these systems are very restricted (Wilson, Hassell & Godfray 1996). Whether this applies for systems formed by brood parasites and their hosts needs yet to be explored.

The topic is particularly timely because some brood parasites species have expanded their geographical range (Robinson *et al.* 1995a; Cruz *et al.* 1998) and are attacking new host populations and species. From a conservation point of view it is crucial to understand the dynamics of invasions and under which conditions a parasite persists in a new host or host community and/or leads to its decline and eventual extinction.

The population dynamics of host–brood parasite systems were studied in detail by May & Robinson (1985), who examined generalized and specialized parasitism in separate models. In their models, the consequences of parasitism for the host population are given in terms of the probability of parasitism and mortality rates. These authors represented the number of offspring fledged in parasitized and unparasitized nests by their average, regardless of the distribution of parasitic eggs per nest, and included minimum known biological properties of specific brood parasite systems. We introduce a degree of realistic complexity and develop new models including a generalized May and Robinson model that combines both parasitic species, using these extended models to test for the robustness of May and Robinson's predictions.

Our system is formed by the shiny cowbird *Molothrus bonariensis*, the screaming cowbird *M. rufoaxillaris*, and the nonparasitic bay-winged cowbird *Agelaioides badius*. Note that *A. badius* has been treated as a species of *Molothrus* until recently (Lanyon 1992; Lanyon & Omland 1999). Shiny cowbirds parasitize at least 214 species (Ortega 1998), while screaming cowbirds parasitize almost exclusively the bay-winged cowbird, which is also parasitized by shiny cowbirds (Fraga 1998). This system has characteristics that can be expected to influence population dynamics. We pay attention to the following facts: (i) females lay at most one egg per day; (ii) when the total clutch (host plus parasite) exceeds a maximum, the host deserts (Fraga 1998); and (iii) parasites peck and puncture host eggs (Fraga 1998). These properties are not rare: they are present in most avian host–brood parasite systems. We study the importance of these properties by confronting our model to the model of May & Robinson (1985) that does not include them. We also study the persistence of a host species that is attacked by two parasitic species by comparing the behaviour of a three-species model with the host–specialist model.

A cowbird community: generalist–specialist–host

The bay-winged cowbird (the host) occupies regions of central and southern South America. The screaming cowbird (the specialist) overlaps extensively with the host, while the shiny cowbird (the generalist) overlaps with both species everywhere (Fraga 1998; Ortega 1998).

Bay-winged cowbirds breed from late October to mid March (Fraga 1998). Their breeding season overlaps totally with that of the specialist, but only partially with the generalist, which breeds from late September to late January (Ortega 1998).

Fraga (1998) found that the majority of bay-winged cowbird nests in his study area were parasitized by screaming cowbirds while less than 25% were parasitized by shiny cowbirds (see also Hoy & Ottow 1964; Mason 1980), and that more than 80% of the nests were multiply parasitized. There is no evidence for departures from randomness in the distribution of parasitic attacks.

Birds take at least a day to produce an egg that if not laid cannot be stored. This reduces the maximum number of eggs laid. Total egg laying also depends on the duration of the breeding season and the maximum number of eggs a parasite female can produce in a season.

Beyond a total (host plus parasite) clutch size of about eight eggs hosts abandon the nest (Hoy & Ottow 1964; Fraga 1998).

Both screaming and shiny cowbirds puncture host eggs when they parasitize nests (Fraga 1998; Massoni & Reboreda 1998; Mermoz & Reboreda 1999). Screaming cowbirds puncture on average 0·63 host eggs (Fraga 1998) and shiny cowbirds 0·65 host eggs, per parasitic event (Massoni & Reboreda 1998; Mermoz & Reboreda 1999). In nests containing eggs of two or three species, parasitic females peck eggs indiscriminately. However, because parasitic eggs have a more rounded shape and a thicker eggshell than host eggs (Spaw & Rower 1987; Rahn, Curran-Everett & Booth 1988; Mermoz & Ornelas 2004) they have a lower probability of puncture (Mermoz *et al*. 1999). We assume that the number of parasite eggs lost by punctures was negligible.

Population dynamics model

We consider the density of the generalist constant (henceforth noted G). This is justified because the generalist attacks many species, and hence its density is not coupled to that of any specific host. We do not include density dependence on the host population in order to highlight the influences of the interactions with other species. This is further justified because the impact of parasitism appears to be extremely strong for this host (Fraga 1998), probably dominating other regulatory forces. The dynamics of the system are described by two equations, one for the number of host females (N_t),

which equals the number of nests, and the other for the number of specialist females (P_t).

Cowbirds have a relatively discrete reproduction period, so that their dynamics are naturally described on a yearly basis. Therefore, the model uses discrete-time difference equations. It assumes that host females have one brood each year, and that host females as well as parasite females hatched in year t become fully mature in year $t + 1$. The host and parasite adult mortality rates (μ and ν, respectively) are age-independent. The survival rate of chicks (from hatching to first year) in unparasitized nests (s) is assumed to be independent of their own number. Similarly, the survival rates of host chicks in parasitized nests (s') and of the specialist chicks (s_p) are independent of the nest mates. Survival for the host and the parasite during the first year is much lower than for subsequent years (see Table 1).

The model assumes that a parasitic event, also called a nest attack, always results in the laying of a parasitic egg in the nest, and may be accompanied by a puncture with a specified probability. Both parasitic species distribute attacks at random and independently of each other. The probability that a nest is attacked r times by each of the parasite species is given by a Poisson distribution with mean λ or λ_G, respectively, the mean number of attacks by specialist and generalist. $\lambda = N_a/N_t$, where N_a is the total number of specialist attacks.

Females cannot lay more than one egg in a day and T eggs per season. This can be taken into account by assuming that the number of attacks per female parasite follows a type II functional response (Hassell &

Table 1. Notation and some values of parameters that come into play in the model developed in this paper (Fraga 1998)

Host parameters		
s	Survival from hatching to first year	0·39 (unparasitized nests)
s'		0·34 (parasitized nests)
b	Number of host eggs at the time of hatching	3·75 (unparasitized nests)
b'		2 (parasitized nests)
σ	Number of female hosts reared to reproductive	
σ'	adulthood $\sigma = (1/2)sb$, $\sigma' = (1/2)s'b'$	
μ	Adult probability of dying during the year	0·24
D_A	Lifetime of a nest available for parasitism	≤ 16 days
D_S	Duration of the breeding season	120 days
x	Fraction of nests in laying-period among available nests	$\leq 0·25$
Specialist parasite parameters		
T	Number of eggs produced each year by one female parasite	Presumably in [20–50]
s_p	Survival of parasite chicks from hatching to first year	0·275
p	Number of parasitic eggs in a nest	2·54
σ_p	Number of female parasites reared to reproductive adulthood	
ν	Adult probability of dying during the year	0·62–0·84
t	Egg-production time in days	1
$P_a(0) = e^{-\lambda}$	Probability that a nest escapes parasitism	0·2
a	Searching efficiency and $A \equiv D_A/D_S$	a is unknown
A		
Generalist parasite parameters		
$\bar{G}$	Population density	Unknown
$e^{-\lambda_G}$	Probability that a nest escapes parasitism	0·76
T_G	Number of eggs laid each year in nests of the host under consideration	unknown
a_G	Searching efficiency and $A_G \equiv (a_G D_A)/D_S$	a_G is unknown
A_G		

May 1973) in which the traditional handling time term represents the time to mature an egg (t_m)

$$\frac{N_a}{P_t} = \frac{ATN_t}{1 + At_mN_t} \quad \text{where} \quad A \equiv \frac{aD_A}{D_S} \qquad \text{eqn 1}$$

D_S is the duration of the breeding season (in days). Each nest is available for parasitism (in its laying and incubation period) for D_A days, so that there are in total ND_A/D_S nests available for parasitism each day. Henceforth t_m will be set either to 1 (day) or to 0 (representing a case in which there is no limit to egg production). Finally, a is the searching efficiency of the parasite.

An expression similar to eqn 1 is used for the generalist with a_G being the searching efficiency and T_G being the number of eggs produced by a generalist female laid in nests of the host under consideration. In the following, we use

$$G \equiv T_G \bar{G} \qquad \text{eqn 2}$$

where G is the total number of eggs laid in host nests by the generalist population. The fact that the breeding season of host and parasite may not overlap completely (Table 1), can be taken into account within this parameter combination. G increases with the overlap of seasons.

Whenever the total number of eggs in a nest exceeds *MBS* (Maximum Brood Size), the nest is deserted, and deserting parents do not re-nest (see the section on the impact of the generalist).

At each attack, the parasite female punctures or removes a host egg with frequency *Pun*.

Table 1 lists symbols and their meaning. The dynamics of host and specialist in the presence of a generalist is described by the following equations

$$\begin{cases} N_{t+1} = (1 - \mu + \frac{1}{2}sbe^{-\lambda}e^{-\lambda_G} + \frac{1}{2}s'g(\lambda, \lambda_G) \\ \qquad + \frac{1}{2}s'g(\lambda_G, \lambda) + \frac{1}{2}s'\hat{g}(\lambda, \lambda_G))N_t \\ P_{t+1} = (1 - \nu)P_t + \frac{1}{2}xs_p(f(\lambda, \lambda_G) + \hat{f}(\lambda, \lambda_G))N_t \end{cases} \qquad \text{eqn 3}$$

The equation for the number of nests at year $t + 1$ (first equation in eqn 3) results from the number of nests at year t, subtracting the adult females that died during the year and adding yearling females. The latter are described by the last four terms in this equation that correspond to yearling females emerging from nests that have: (i) not been attacked; (ii) been attacked exclusively by the specialist; (iii) been attacked exclusively by the generalist; and (iv) been attacked by both parasites. Each of the four terms is the product of the sex ratio (1 : 2), the survival rates of the chicks, and the number of chicks hatching weighted by the probability that the nest be parasitized and not deserted. The joint probability that the nest is parasitized and not deserted is given by functions $g(\lambda, \lambda_G)$, $g_G(\lambda, \lambda_G)$, and $\hat{g}(\lambda, \lambda_G)$, respectively, for the last three categories of nests, see (ii) to (iv) above. In fact $g_G(\lambda, \lambda_G) = g(\lambda_G, \lambda)$ as generalist and specialist parasites are assumed to have identical parasitic behaviour.

The number of specialist females at year $t + 1$ is the sum of the number of adults that survive the year plus the female yearlings from nests attacked exclusively by the specialist and from nests attacked by both parasites (second equation in eqn 3). The functions $f(\lambda, \lambda_G)$ and $\hat{f}(\lambda, \lambda_G)$ represent, respectively, the number of specialist eggs hatching in the latter two categories of nests weighted by the probability that the nest be parasitized and not deserted. Finally, x is the fraction of available nests in their laying period.

We now address in detail the four functions determining the joint probability that the nest is parasitized and not deserted. In a nest that received r attacks by the specialist and q by the generalist, the total number of eggs is the sum of $b - (r + q)$ *Pun* host eggs plus $r + q$ parasitic eggs. When all host eggs have been punctured, there remain $r + q$ eggs in the nest. Whenever *MBS* is exceeded the brood is lost. The function f and g give the number of host and specialist chicks, respectively. As already stated, r and q are drawn from independent Poisson distributions. This yields

$$\begin{cases} g(\lambda, \lambda_G) = e^{-\lambda_G}e^{-\lambda}\sum_{r\geq1}\Theta[b - rPun]U[MBS - \Theta[b - rPun] - r]\frac{\lambda^r}{r!} \\ \hat{g}(\lambda, \lambda_G) = e^{-\lambda_G}e^{-\lambda}\sum_{r\geq1}\sum_{q\geq1}\Theta[b - (r + q)Pun]U[MBS \\ \qquad - \Theta[b - (r + q)Pun] - r - q]\frac{\lambda_G^q}{q!}\frac{\lambda^r}{r!} \\ f(\lambda, \lambda_G) = e^{-\lambda_G}e^{-\lambda}\sum_{r\geq1}U[MBS - \Theta[b - rPun] - r]\frac{\lambda^r}{(r - 1)!} \\ \hat{f}(\lambda, \lambda_G) = e^{-\lambda_G}e^{-\lambda}\sum_{r\geq1}\sum_{q\geq1}U[MBS - \Theta[b - (r + q)Pun] \\ \qquad - r - q]\frac{\lambda_G^q}{q!}\frac{\lambda^r}{(r - 1)!} \end{cases}$$
$$\text{eqn 4}$$

where $U(x) = 1$ if x positive, 0 otherwise expresses the *MBS* condition, and $\Theta(x) = x$ if x positive, 0 otherwise expresses the puncture effect.

We now introduce a generalized version of the May and Robinson model where specialist and generalist host uses are combined into a single set of equations. These authors assumed that each parasitized nest gives rise to a fixed number of hosts (b') and adult parasites (p') in the next generation, independently of the number of attacks.

$$\begin{cases} g_{MR}(\lambda, \lambda_G) = b'(1 - e^{-\lambda})e^{-\lambda_G} \\ \hat{g}_{MR}(\lambda, \lambda_G) = b'(1 - e^{-\lambda})(1 - e^{-\lambda_G}) \\ f_{MR}(\lambda, \lambda_G) = p(1 - e^{-\lambda})e^{-\lambda_G} \\ \hat{f}_{MR}(\lambda, \lambda_G) = p(1 - e^{-\lambda})(1 - e^{-\lambda_G}) \end{cases} \qquad \text{eqn 5}$$

Note that here neither the puncture effect nor nest desertion are included, but this new model differs from the $Pun \to 0$, $MBS \to \infty$ limit of eqn 4 in the fact that the number of chicks reared to maturity is now set to a constant. Substituting eqn 5, eqn 3 simplifies to:

$$\begin{cases} N_{t+1} = (1 - \mu + (\sigma - \sigma')e^{-\lambda}e^{-\lambda_G} + \sigma')N_t \\ P_{t+1} = (1 - \nu)P_t + x\sigma_p(1 - e^{-\lambda})N_t \end{cases} \qquad \text{eqn 6}$$

where $\sigma = (1/2)sb$, $\sigma' = (1/2)s'b'$ and $\sigma_p = (1/2)s_pp$ (see Table 1 for notations). May & Robinson (1985) studied this model in two particular cases, i.e. when one or the other parasite is not present in the system (note that in their notations, $sb = \gamma$, $s_pp = \Gamma$, $s'b' = \gamma'$ and $x = 1$).

Impact of a generalist on a host–specialist community

Does the presence of a generalist parasite change the conditions of stability of the host–specialist system? To answer this question, the stability boundaries of the host–specialist system (eqn 3 with $G = 0$) were compared with those of the three-species system ($G > 0$), mainly numerically by iterating eqn 3. Stability criteria are computed in the Appendix. We present most of the model's results as stability boundaries in terms of μ and s (the host's survival to first year and mortality rate), which have a crucial influence on stability. Similar conclusions to those presented here could have been drawn from a plot in the (μ, s')-plane. Stability plots for various μ- and s-values were generated keeping the other parameters constant. Steady states were usually rapidly reached ($t \approx 100$). In some cases, the simulations resulted in stable limit cycles.

Figure 1 shows the stability boundaries for $T = 50$ (the largest realistic value for the specialist cowbird species), and $G = 0$ (i.e. in the absence of the generalist) or 20 eggs laid by the generalist in host nests (other
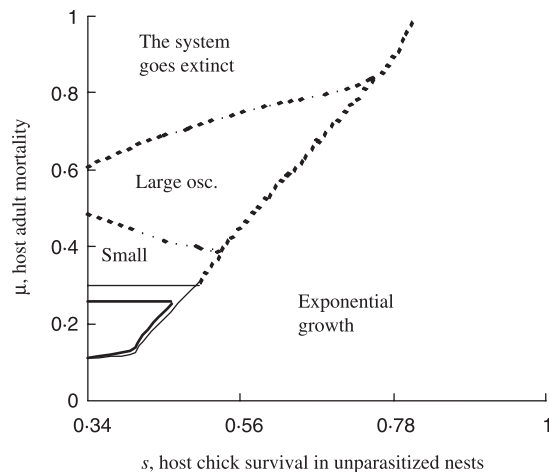
parameter values as in Table 2). In the case with $G = 0$, we show the region of small-amplitude limit cycles defined arbitrarily as the region where both populations oscillate at a stable amplitude smaller than 100 individuals. This region can be combined with the stable equilibrium region when studying the persistence of a real biological system. Then the persistence of the three-species system occurs for μ broadly in $[0\cdot1; 0\cdot45]$ and s in $[0\cdot34; 0\cdot5]$. These are realistic values for the cowbird system (Table 1). Further simulations have shown that the conditions for coexistence shrink if MBS or Pun increases or if T decreases.

For comparison, Fig. 2 shows the stability boundaries for a simplified model excluding nest desertion, egg puncture and egg-maturation time ($MBS = \infty$, $Pun = 0$, and $t_m = 0$). This is in fact the generalized May & Robinson model (1985) of eqn 6. We ran the model with $G = 0$, 5, or 20. As G increases from 0 to 5 the stability boundary is displaced towards larger s. Increasing generalist parasitism further has a dramatic impact on coexistence compared with the previous model,

Table 2. Parameter values used in numerical simulations unless otherwise specified

$A = A_G$	$0\cdot2$
s_p	$0\cdot27$
s'	$0\cdot34$
b	4
b'	2
p	$2\cdot54$
x	$0\cdot2$
ν	$0\cdot7$
Pun	$0\cdot6$
MBS	7
T	50
t_m	1

Fig. 1. Conditions for coexistence of host and specialist parasite (thin line) and host, specialist and generalist parasites ($G = 20$, thick line). This is the result of numerical iteration of eqn 3 with parameter values of Table 2. The x-axis is the survival of host chicks to maturity in unparasitized nests. This cannot be lower than the corresponding survival rate in parasitized nests, namely $0\cdot34$. There is only a small region of stability delimited by the two thin lines that gets even smaller when generalist parasites come into play (thick lines). At low μ or high s, both host and specialist parasite populations grow exponentially. At high μ they both go extinct. Between these two extremes, as mortality increases and s stays lower than $0\cdot78$, the system goes from the stability region to a region of small and then large stable limit cycles. This region is shown on the figure in case with $G = 0$.
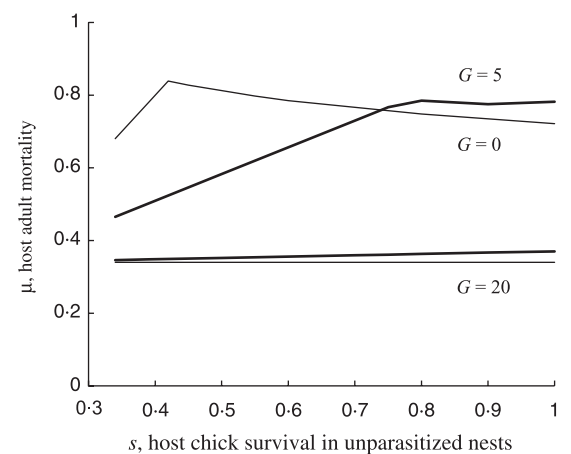

Fig. 2. The May and Robinson model leads to a region of stable coexistence of host and specialist parasite lying between the lower horizontal line ($\mu = s = 0\cdot34$) and the thinner line. In presence of the generalist parasite the lower bound does not change, but the upper bound moves right and down, see the intermediate line $G = 5$. For $G = 20$ (thicker line) coexistence is hardly possible and the specialist and host populations are driven to extinction by the generalist parasite.

reducing the stability region to a very small area. Under this model, stability is impossible for $G > 20$ eggs.

Parasitic cowbirds have a very high fecundity. Scott & Ankney (1980) estimated that the annual fecundity of brown-headed cowbirds was 40 eggs (but see Alderson *et al.* 1999; Woolfenden *et al.* 2003). Similarly, Kattan (1993) estimated that shiny cowbirds could lay up to 120 eggs during the breeding season, but his study was conducted in the tropics, where the breeding season is twice as long as in temperate regions. We assumed that values for the number of eggs laid by the specialist female (T) were in the range of 20–50 eggs. In our model (Fig. 1), apart from the largest values in this interval, the three-species system cannot persist (simulations give a lower limit of 39 eggs). Moreover, the stability is restricted to a rather limited range of μ- and s-values; the smaller T, the smaller this range.

Consider now a population of specialist parasites that lay $T = 50$ eggs per female each year and a population of generalist parasites that lay $G = T_G G = 3·8$ eggs each year. The latter is fixed at a low value that leads to a percentage of host nests parasitized by the generalist of 25%, which is what Fraga (1998) observed for cowbirds in natural conditions (Table 1). The most important result is that the stability diagram obtained by simulation differs little from Fig. 1 when $G = 0$. Furthermore, the resulting percentage of host nests parasitized by the specialist is 98·5% (as observed for the cowbird system by Fraga 1998). The simulation predicts that the fraction of over-crowded nests that are deserted is 0·03, and thus the number of successful nests per host female is very close to one. This suggests that further assumptions on the occurrence of second nest attempt would not have a large impact on stability.

We have shown in this section that the higher the generalist parasitism (G), the more restrictive the conditions of persistence of the community. Generalist parasitism soon reaches a level at which the host and the specialist are driven to extinction whatever their parameters. This occurs when the generalist lays a total of 36 eggs or more (when a single specialist female lays up to 50 eggs), according to our simulation, to be compared with 20 eggs when none of the three factors under consideration in this paper are included. The generalist parasite population persists in any case as it attacks other hosts. Note that there is no constraint on invasions of the host–specialist community by a generalist, because the generalist population density does not depend on the two others. The three-species system resulting from such an invasion persists or not depending on parameter values. In our model, each of the three factors, namely egg-maturation time, brood size limitation, and egg puncture, decreases the impact of generalist parasitism.

Invasion of a specialist into a host–generalist community

So far we gave priority to the specialist–host system and examined how a generalist alters the resulting conditions for stability. Now we turn to the opposite question: given a two-species system formed by a generalist and one of its hosts, can a specialist expanding its range from a region where it survives in sympatry with the host join in and coexist with the previous two species?

STABILITY OF THE HOST–GENERALIST SYSTEM

The critical level of generalist parasitism that a host population can withstand before being driven to extinction can easily be computed. Recall that in the absence of a specialist parasite the model is described by

$$\begin{cases} N_{t+1} = N_t F(N_t) \\ F(N_t) = 1 - \mu + \frac{1}{2} s b e^{-\lambda_G} + \frac{1}{2} s' e^{-\lambda_G} \sum_{r \geq 1} \Theta[b - rPun] \frac{\lambda_G^r}{r!} \end{cases}$$
eqn 7

where $F(N_t)$ is the host reproductive rate. Note that $F(N_t)$ depends on N_t through λ_G. Below a critical level of generalist parasitism, the host grows exponentially, and above this level it is driven to extinction. The critical level of generalist parasitism can be expressed either as the number of eggs a generalist female lays in the host nests, or as a probability of attack $p_G = 1 - e^{-\lambda_G}$. $[p_G]_{critical}$ and $[G]_{critical}$ can be plotted as functions of adult host mortality μ (Fig. 3). It is interesting to compare these results with the basic host–generalist model with no egg puncture, and no limitations in either egg-maturation time or brood size (May & Robinson 1985). Figure 3 illustrates that host population persistence depends on generalist parasitism in both cases but it does so in a less sensitive way when more biological realism is included.

INVASION CONDITIONS

The goal of this section is to analyse the outcome of an invasion of a host–generalist system by the specialist. This could be assessed by setting that the host population is at equilibrium in the presence of the generalist, and that invading specialists arrive in very low numbers. An invasion can be considered successful whenever the specialists increase in numbers, i.e. their growth rate is larger than unity (Wilson *et al.* 1996). In models where there is no preinvasion equilibrium host density, invasion succeeds when

$$\lim_{\Gamma \to \infty} \frac{1}{\Gamma} \sum_{t=0}^{\Gamma-1} \ln\left(\frac{P_{t+1}}{P_t}\right) > 0 \qquad \text{eqn 8}$$

In a constant environment, i.e. in absence of stochasticity, inequality 8 amounts to checking that the long-term growth rate $\Gamma^{-1}(\ln P_\Gamma - \ln P_0)$ takes a finite positive value as time, Γ, approaches infinity (e.g. in Metz, Nisbet & Geritz 1992).

We first study invasion with neither egg punctures nor nest desertions included (eqn A12). This shows the impact of the biological process that, according to the results in the previous section, has the strongest
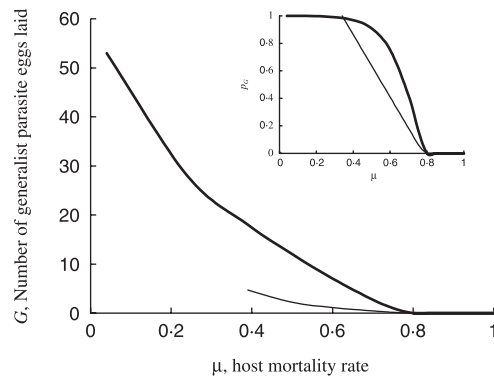
Fig. 3. The critical parasitism level G and the critical probability of parasitism, p_G (inset) as a function of adult host mortality μ. Critical means that above this threshold the host falls to extinction. Upper curves (thick lines) are obtained numerically from our model, which is compared with the May and Robinson model (lower thin lines calculated analytically). For the latter, the quantities plotted here are not defined when mortality is lower than survival in parasitized nests (0·34), a limitation that does not exist in our model. If host mortality rate is, say, 0·4 the critical level of generalist parasitism is 18 eggs laid (and only five in May & Robinson (1985); our model hence predicts a relatively low impact of the generalist on the host community.

impact on the persistence of the system namely, egg-maturation time (letting $t_m = 1$). Linearizing the equations for very small P_t, one gets

$$\frac{P_{t+1}}{P_t} = 1 - \nu + \frac{x\sigma_p ATN_t}{1 + AN_t} \qquad \text{eqn 9}$$

We have shown earlier that in the absence of specialists and above the critical level of generalist parasitism (inequality A14), host density crashes, and that below this level it grows without bounds. This unchecked growth depends on excluding density dependence of the host population other than the effect of specialist parasitism, that is the variable we wish to explore. The expression in eqn 9 tends to $1 - \nu$ when the host density tends to zero and to $1 - \nu + x\sigma_p T$ when the host density increases without bounds. Combining these limits and inequality 8 shows that the host–generalist system cannot be invaded above the critical level of generalist parasitism, and that invasion succeeds below this level if the reproductive opportunities for the specialist, $x\sigma_p T$ are high enough (recall that x is the fraction of nests available for reproduction, σ_p is the number of chicks reared to adulthood, and T is the number of eggs produced per female each year).

The same tendency according to parasite mortality and reproductive rate is obtained including the three factors described earlier. This result is obtained by computing condition 9 numerically. First some host density dependence is added so that the host population does not rise without bound if the specialist goes extinct. Assuming that density-dependent mortality acts at the end of the season at a rate δ, the equation for the host population (eqn 7) becomes
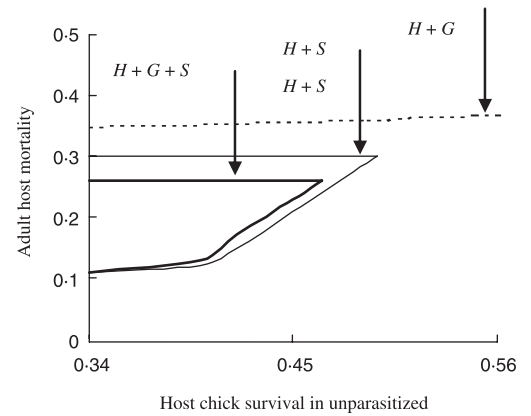

Fig. 4. Conditions for invasion and stability of communities consisting of indicated combinations of host (H), specialist parasite (S), and generalist parasite (G). This is the result of numerical iteration of eqn 3 and 4 with parameter values of Table 2. The dotted line is the boundary above which the host is driven to extinction by the generalist parasite.

$$N_{t+1} = N_t F(N_t) \text{Exp}(-\delta N_t) \qquad \text{eqn 10}$$

with $F(N_t)$ in eqn 7. We use $\delta = 10^{-10}$ (i.e. very large carrying capacity). The specialist is inoculated at very low population level (e.g. $P_0 = 10^{-8}$) to a host population in equilibrium. The coupled equations for host and specialist parasites are iterated for at most 10 000 years. The density-dependent mortality rate does not change the main conclusions on invasion (comparing $\delta = 0$ and $\delta = 10^{-10}$) and holds for larger values of δ. The introduction of the density-dependent mortality, δ, has the trivial effect of stabilizing a host population that would otherwise grow exponentially, at the carrying capacity. For these reasons this factor has not been included sooner in the model.

Numerical results show that the host–generalist system can be invaded by the specialist and the three-species community is dynamically stable. Figure 4 shows the region of interest (lower left quarter of Fig. 1) except that the boundary in the host–generalist system (between host expansion and host extinction) is added. Similarly, our model implies that the boundary depends little on the generalist parasite efficiency (more eggs laid, G, or larger searching efficiency, a_G), in the region of parameter space of interest.

To conclude, the invasion region by the specialist parasite coincides with the stability region of three-species community. This region is small, which suggests that the establishment of such a community as observed in the *Molothrus* cowbirds is a rare event.

Discussion

We analysed the dynamics of a host–brood parasite community formed by a generalist and a specialist brood parasite with a host parasitized by both. We include realistic features of a known system that seem intuitively to be important for population dynamics.

We are conscious that perhaps the most important contribution of theoretical modelling to biological thinking is extracting general principles from streamlined, simple models of great generality, and that adding complexity has a cost in terms of the heuristic contribution models make, but we trade this cost off against working with models that cannot make reliable predictions because crucial constraints of the real systems are missing.

We used as a benchmark a series of models developed by May & Robinson (1985), and built more complex models. The features of the real system that we added are: (i) parasite females produce no more than one egg per day; (ii) parasite females puncture (or remove) host eggs; and (iii) hosts desert overcrowded nests. While May and Robinson's model did not include nest abandonment and egg puncturing explicitly, their model was sensitive to these two parameters through their impact on survival data. In the present paper, other potentially significant properties were ignored. Among these, we assumed that the generalist population is entirely decoupled of the other two and did not implement a safe fraction of the host's nests in the temporal refuge resulting from nonoverlapping of reproductive seasons.

Our main findings were that (1) persistence is much restricted when the three features mentioned above are included in the model, the influence of the specialist's maximum rate of egg production and maximum seasonal fecundity being more important in constraining the conditions for persistence than the other two (M. Ney-Nifle unpublished). As these aspects had been ignored by pre-existent brood parasitism models, the dynamics for invasions and stability suggested by previous models do not give an accurate picture. It would be impossible to understand, and hence predict and intervene in ecological invasions such as those currently on course by shiny cowbirds in North America using models that exclude these crucial properties.

Comparing the three-species system with a two-species specialist–host model shows that (2) normally, the invading generalist parasite has a moderate impact on the coexistence of host and specialist, but at high density of the generalist, specialist and host can be driven to extinction. The analysis of the invasion of the host–generalist system by the specialist suggests that (3) invasion is successful only in the (restricted) stability boundaries of the three-species system. The dynamics of invasions were examined by comparing the three-species system with the two possible parasite–host systems. The results are intuitively obvious: Introduction of a generalist has only moderate effect on the persistence of a specialist–host system. When instead a specialist is introduced to a generalist–host system, the specialist often does not prosper, unless all the parameters are within the limited region where the three-species system is stable.

Interestingly, the range of parameter values where the coexistence of the three species is possible includes those that have been measured in field studies on cowbirds (Fraga 1998). The system is only stable in a small region. This suggests that the real system may be very vulnerable to perturbations: particularly any factor affecting host chick survivorship in unparasitized nests or host adult mortality could destabilize the system leading to local extinctions.

A factor that determines the persistence of systems, including the specialist, is the number of eggs that females can lay in available nests. Two parameters control this number: rate of egg production ($1/t_m$) and maximum seasonal fecundity (T). Together these parameters set the asymptote of the type II functional response. The destabilizing influence of type II functional responses in host–parasitoid systems is well known (Hassell & May 1973). Nevertheless, it is customary to assume that the asymptote is sufficiently high as to allow simplifying the models by assuming linear functional responses. The present study suggests that in brood parasitism, for realistic values of T and t_m the destabilizing influence of type II functional responses could be so important that ignoring it would lead to misleading results.

Our model includes some simplifications on the biology of the three cowbird species. First, in most of this work we ignored intraspecific density-dependent processes. Clearly, the inclusion of such factors would expand the stability boundaries of the model. Density dependence was ignored on the grounds that little information is available on intraspecific competition in cowbirds and that including it would obscure the influence of interspecific interactions. The fact that independently measured field estimations of parameter values fall inside the stability boundaries suggests that intraspecific competition is not a major feature of the three-species interaction. Secondly, we simplified the egg puncture process by assuming that, when visiting an already parasitized nest, parasite females puncture only host eggs. In fact, parasites are known sometimes to peck parasite eggs (Fraga 1998; Mermoz *et al.* 1999). The inclusion of punctures on parasite eggs would result in an increase in the number of host eggs and a decrease in the number of specialist and generalist eggs. However, most likely, this will have a moderate influence in the dynamics of the system because: (i) while host eggs are punctured in all parasitized nests, parasite eggs are only affected in multiply parasitized nests, and (ii) parasite eggs have a thicker eggshell than host eggs resulting in a lower probability of being destroyed (Mermoz *et al.* 1999). We also assumed that hosts deserting an over-crowded nest do not re-nest. In natural conditions this is not always the case, especially when nest desertion occurs early in the breeding season. This difference between the real system and the model assumptions is also likely to have a moderate impact. In our model, the predicted frequency with which nests were abandoned was quite low. On the other hand, our model did not consider nest predation. This over-estimation of nest success should counterbalance, at least partially,

the under-estimation incurred by ignoring re-nesting. Finally, we assumed that all the females and males breed. This assumption could be invalid because it is known that this host has individuals that do not breed and help with parental duties to reproductive pairs ('helpers at the nest', Fraga 1991). There is little information about the sex and proportion of helpers in the host population (Fraga 1991). One of the favoured hypotheses for explaining helping behaviour is that helpers do not breed independently because there are no territories available (habitat saturation, Hatchwell & Komdeur 2000). If this is also the case in the host, our assumption holds for low population densities.

Cowbird species range from partial specialists to broad generalists. This has broad consequences for the establishment of two-species systems: while the stability characteristics of the host–generalist system will depend mostly on the characteristics of the generalist species, stable host–specialist systems are only possible for a restricted set of parameter values. Invasion of the host–generalist system by the specialist is only possible under the restricted conditions that lead to the stability of the three-species systems. Invasion by a generalist is always possible, but outside the three-species stability boundaries it will lead to the instability of the host–specialist system. This might have little impact on the generalist population while leading the other two species to extinction.

The model presented here can be applied to the study of a three-species community consisting of two generalist brood parasites sharing a host. This situation has recently arisen in North America, where generalist brown-headed cowbirds have started to compete for the use of hosts with the invading generalist shiny cowbird (Cruz *et al.* 1998). According to our model, the crucial parameter for coexistence is the sum of the number of eggs laid by each parasite species in the host nests that they share. The larger this number, the more likely the extinction of the host. Because the impact of the different generalist parasite species on host population is additive in the model, the arrival of a new generalist parasite will have a strong and immediate impact on host populations.

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Appendix

The first section of this Appendix deals with two-species (specialist and host) communities and the second with three species (specialist, generalist, and host) communities.

HOST−SPECIALIST MODELS

Throughout this study we use the two-species model proposed by May & Robinson (1985; our eqn 6) as a reference, and study the effects of adding three different realistic traits that are known to apply in real communities.

The two-species system is obtained by setting the influence of the generalist as nil ($G = 0$) in eqn 3. The resulting simplification is shown below.

$$\begin{cases} N_{t+1} = (1 - \mu + \tfrac{1}{2} sbe^{-\lambda} + \tfrac{1}{2} s' g(\lambda)N_t \\ P_{t+1} = (1 - \nu)P_t + x \tfrac{1}{2} s_p f(\lambda)N_t \end{cases} \qquad \text{eqn A1}$$

(see notation of Table 1) where functions g and f (eqn 4) are

$$\begin{cases} g(\lambda) = e^{-\lambda} \sum_{r \geq 1} (b - rPun)\dfrac{\lambda^r}{r!} \\ f(\lambda) = e^{-\lambda} \sum_{r \geq 1} \dfrac{\lambda^r}{(r-1)!} \end{cases} \qquad \text{eqn A2}$$

First we proceed to the stability analysis in two steps by getting the equilibrium points and then the conditions for stability against small (linear) perturbations. In parallel to these analytical derivations, we also performed extensive numerical studies and verified that we get the same stability diagram. Calculations were done with the software Mathematica (Wolfram 1999).

Stability when parasites cannot lay more than an egg a day

Setting $\{N^* = N_{t+1} = N_t; P^* = P_{t+1} = P_t\}$ in eqn A1 with,

$$\begin{cases} g_{MR}(\lambda) = b'(1 - e^{-\lambda}) \\ f_{MR}(\lambda) = p(1 - e^{-\lambda}) \end{cases} \qquad \text{eqn A3·1}$$

where

$$\lambda = \frac{ATP_t}{1 + At_m N_t} \qquad \text{eqn A3·2}$$

one gets

$$\lambda^* = Ln\left(\frac{\sigma - \sigma'}{\mu - \sigma'}\right) \qquad \text{eqn A4}$$

and

$$\begin{cases} ATP^* = \lambda^*(1 + tN^*) \\ N^* = \dfrac{\nu \lambda^*}{ATx\sigma_p(1 - e^{-\lambda^*}) - \nu At\lambda^*} \end{cases} \qquad \text{eqn A5}$$

It must be noted that the necessary condition $0 < e^{-\lambda} < 1$, imposes

$$\sigma' < \mu < \sigma \qquad \text{eqn A6}$$

where we used the fact that the number of host chicks reared to maturity must be lower in an parasitized than in a unparasitized nest, i.e. $\sigma' < \sigma$. The inequalities in eqn A6 are necessary at equilibrium because if the

right-hand side of (eqn A6) is violated, the host's reproductive rate in unparasitized nests is lower than the mortality rate, and the population collapses even in the absence of parasitism, while if the left side of (eqn A6) is not verified mortality rate is lower than the reproductive rate in parasitized nests, and the host population grows without bounds.

Following standard techniques (Edelstein-Keshet 1988), we now compute the four elements of the jacobian matrix, J, after linearization of eqn A1. Stability conditions are given by $1 > \text{Det}(J) > \text{Trace}(J) - 1$, which yields

$$\begin{cases} 1 - \dfrac{\mu - \sigma'}{\sigma - \mu}\lambda\left((1 + \sigma - \mu) + \dfrac{t_m\lambda}{Tx\sigma_p}(1 - \nu)(\sigma - \sigma')\right) > 0 \\ Tx\sigma_p(\sigma - \mu) - t_m\nu(\sigma - \sigma')\lambda > 0 \end{cases} \quad \text{eqn A7}$$

When $t_m = 0$ in eqn A7, one recovers the May and Robinson model (1985), for which the second inequality is trivially satisfied. The only parameters involved in the remaining stability condition are μ, σ, and σ'. In the general case, in which the unrealistic ability of generating eggs instantaneously is excluded and then $t_m > 0$, there are additional parameters involved, although the parasite searching efficiency A is notably absent. eqn A7 show that there is a critical value of the parasite's total fecundity, T, below which none of the inequalities are verified and hence equilibrium is not possible. The stability frontiers in the (μ, σ)-plane are obtained from the inequalities in eqn A6 and A7, the latter being solved numerically when no analytical expressions are available.

Stability when brood size is limited or when parasites puncture host eggs In this case the equilibrium state $P*$ is the solution of the first equation in A1 (after $N*$ is eliminated), that is,

$$2\mu = \sigma e^{-ATP} + \sigma'g(ATP) \quad \text{eqn A8}$$

which can be solved numerically.

The stability conditions resulting from the inequalities $1 > \text{Det}(J) > \text{Trace}(J) - 1$ lead to the results given in the text.

A HOST–SPECIALIST–GENERALIST MODEL

For general forms of the functions f and g (eqn 4) there are no analytical solutions at equilibrium. Therefore the two coupled equations have to be iterated numerically. The stability boundaries, however, can be inferred analytically in a particular case that is used in the section on invasion of the host–generalist community by a specialist parasite.

The stability of the three-species system can also be explored taking into account the constraint in egg-production time but leaving out puncture and limited brood size factors. In this case, the system simplifies to

$$\begin{cases} N_{t+1} = (1 - \mu + \sigma e^{-\lambda}e^{-\lambda_G} + \sigma'(1 - e^{-\lambda}e^{-\lambda_G}))N_t \\ P_{t+1} = (1 - \nu)P_t + x\sigma_p(1 - e^{-\lambda})N_t \end{cases} \quad \text{eqn A9}$$

where λ and λ_G are functions of N_t and P_t (see eqn A4) and

$$\lambda_G = \dfrac{A_G T_G \bar{G}}{1 + A_G t_m N_t} \quad \text{eqn A10}$$

Letting $N_t = N*$ and $P_t = P*$ in eqn A9 in order to derive the equilibrium points, leads to eqn A8 (obtained in absence of generalist parasitism) with

$$e^{-\lambda*} = \dfrac{\mu - \sigma'}{\sigma - \sigma'}e^{\lambda_G^*} \quad \text{eqn A11}$$

The second equation in A9 can be solved in $N*$ numerically. The first equation in A9 is solved in $P*$ by straightforward substitution of the solution for $N*$. The stability conditions (see above) are then checked numerically.