

The impact of song learning on the evolution of brood parasitism

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Introduction

Obligate interspecific avian brood parasites do not build nests of their own but lay their eggs in the nests of other species. The *Viduinæ* are African songbirds which parasitize estrildid finches. At a young age the males copy the songs of their foster father (Payne *et al.*, 1998) and the females develop a mating preference for males singing a song resembling that of their foster father (Payne *et al.*, 2000). Nicolai (1964) and ten Cate & Vos (1999) propose that these factors have promoted the evolution of their brood-parasitic behaviour. Here we present a recurrence equation model and an individual oriented simulation model to investigate this hypothesis.

Recurrence equation model

Consider a population that consists of birds that are either brood-parasitic, or build nests to raise their own young. Brood-parasitic (or nestbuilding) behaviour of the young is inherited from the mother. The brood parasites as well as the nestbuilders are characterized by either conspecific or heterospecific song. Males express their song by singing, and females by having a mating preference for males singing their song. Females always mate with encountered males that sing the preferred song, and they mate with chance m with encountered males that sing the non-preferred song ($0 \leq m \leq 1$). The number of surviving young of a brood-parasitic female is denoted by E_b , and that of a nestbuilding female by E_n . Newborns either learn the song of the father who raises them with chance s or they do not learn and express the conspecific song with chance $1 - s$. We only follow the dynamics of the females, and assume that those of males are equal. We use n_1 , n_2 , b_1 and b_2 to denote respectively the frequency of nestbuilding females with conspecific song, the frequency of nestbuilding females with heterospecific song, the frequency of brood-parasitic females with conspecific song, and the frequency of brood-parasitic females with heterospecific song. We can derive:

$$\begin{aligned}
 D \quad n'_1 &= E_n \left(n_1(n_1 + b_1 + m(1-s)(n_2 + b_2)) + \right. \\
 &\quad \left. n_2(m(n_1 + b_1) + (1-s)(n_2 + b_2)) \right) \\
 D \quad n'_2 &= E_n \left(m n_1(n_2 + b_2) + n_2(n_2 + b_2) \right) s \\
 D \quad b'_1 &= E_b \left(b_1(n_1 + b_1 + m(n_2 + b_2)) + \right. \\
 &\quad \left. b_2(m(n_1 + b_1) + n_2 + b_2) \right) (1-s) \\
 D \quad b'_2 &= E_b \left(b_1(n_1 + b_1 + m(n_2 + b_2)) + \right. \\
 &\quad \left. b_2(m(n_1 + b_1) + n_2 + b_2) \right) s
 \end{aligned}$$

where

$$\begin{aligned}
 D &= \left(E_n n_1 + E_b b_1 \right) \left(n_1 + b_1 + m(n_2 + b_2) \right) + \\
 &\quad \left(E_n n_2 + E_b b_2 \right) \left(m(n_1 + b_1) + n_2 + b_2 \right) .
 \end{aligned}$$

The stable equilibria for different parameter values are shown in figure 1. In areas with only one stable equilibrium the population will evolve towards this equilibrium, while in bi-stable regions the final population composition depends on the initial conditions. Figure 1 shows what happens if the initial population consists of mostly nestbuilding birds with conspecific song and a few mutant brood parasites with heterospecific song. There is some positive value for the ratio E_b/E_n for which an equilibrium with brood parasites is attained, hence this ratio represents a measure of the difficulty with which brood parasitism evolves. When song develops without learning ($s = 0$), the evolution of brood parasitism is possible if brood parasites have more surviving offspring than nestbuilders ($E_b > E_n$), independent of the mating preference $1/m$. If song learning occurs ($s > 0$), but there is no mating preference based on song ($m = 1$), the condition for the evolution of brood parasitism remains $E_b > E_n$. If there is a mating preference based on song ($m < 1$) and the initial fraction of brood parasites is small, song learning results in more stringent conditions for the evolution of brood parasitism. When the initial fraction of brood

parasites is high, the evolution of brood parasitism is most difficult for intermediate amounts of song learning.

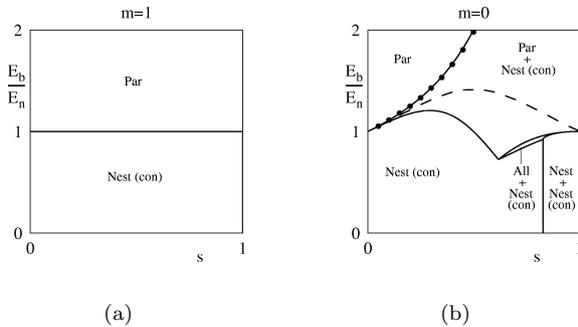


Figure 1: The stable equilibria for the recurrence equation model. Solid lines are bifurcation lines dividing the parameter space in areas of different dynamical behaviour. Equilibria are *Nest(con)* (only nestbuilders singing conspecific song), *Nest* (nestbuilders singing either of the two songs), *Par* (brood parasites singing either of the two songs), and *All* (all possible types of birds). The dotted and dashed lines divide the *Nest(con)* and *Par* bi-stable area into two regions where the initial fraction of brood parasites of respectively 0.1 and 0.5 will either become extinct or invade.

Individual oriented model

The individual oriented computer simulation model is based on similar assumptions as the recurrence equation model. We assume a fixed population size of N females and N males. As before, individuals have either conspecific or heterospecific song. However, instead of being a brood parasite or nestbuilder, birds are assigned a tendency p to lay their eggs parasitically. The p of newborns mutates with probability μ , and the mutation step is drawn randomly from a normal distribution with average 0 and standard deviation σ . The resulting p becomes at most 1.0, and is at least 0.0. We calculate the average p that evolves after many generations for different parameter values (figure 2).

If p is inherited from the mother (figures 2a–c), the results are similar to those of the recurrence equation model for low initial fractions of brood parasites. If p is the average of both parents (figures 2d–f), the results resemble those of the recurrence equation model for high initial fractions of brood parasites. The clear difference in results between the two modes of inheritance of p is due to selection on the males. Since p is not expressed in males, there is no direct selection on p in males. As a consequence, mutants can substantially increase in numbers, and the attracting region of another equilibrium will be more easily reached.

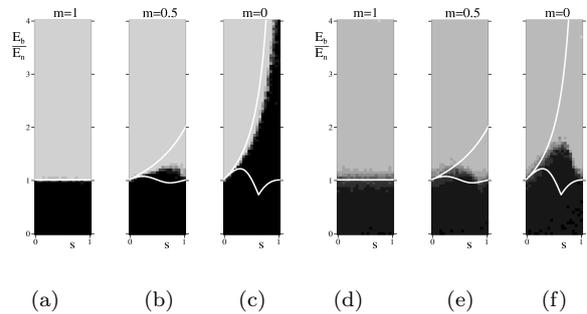


Figure 2: (a–c) The average p that evolves after 100000 generations when p is inherited from the mother. (d–f) The average p that evolves after 500000 generations when p is the average from both parents. Average p 's are shown on a greyscale, darker squares mean lower average p 's. The bifurcation lines that surround the region with the stable equilibria *Nest(con)* and *Par* (see also figure 1) are shown in white. Parameters: $N = 100$, $\mu = 10^{-3}$, $\sigma = 0.1$, $E_n = 1$.

Discussion

We showed that song (preference) learning at a young age forms an obstacle to the evolution of brood parasitism. Several authors have suggested the opposite of our findings (Nicolai, 1964; ten Cate & Vos, 1999). However, they did not take into account that brood parasites are initially in the minority and that this decreases the chance to meet a preferred partner if there is song (preference) learning. Our results confirm that this is an obstacle, although the obstacle can be overcome quite easily if males carry the trait to lay eggs parasitically.

References

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