

This is an electronic appendix to the paper by Ruxton & Broom 2002 Intraspecific brood parasitism can increase the number of eggs that an individual lays in its own nest. *Proc. R. Soc. Lond. B* **269**, 1989-1992.

Electronic appendices are refereed with the text. However, no attempt has been made to impose a uniform editorial style on the electronic appendices.

### **Electronic Appendix A: ESS analysis of the model**

The overall payoff to the host from eggs laid in its own nest is  $R_H$ , where

$$R_H = Hf(H + P) - HC. \quad (\text{A1})$$

Thus, since  $f(x)$  is a decreasing function, the payoff to the host is adversely affected by an increase in the number of parasite eggs. If parasitism was impossible, then the payoff to the host simplifies to

$$R_H = Hf(H) - HC. \quad (\text{A2})$$

Equilibrium occurs when this is maximized with respect to  $H$ . Thus if parasitism is impossible for some reason, then  $H = H_1$  where

$$f(H_1) + H_1 f'(H_1) - C = 0. \quad (\text{A3})$$

Supposing that parasitism is possible,  $R_H$  is again maximized with respect to  $H$  at the ESS. Setting  $H = H_2$ ,  $P = P_2$ , we obtain

$$f(H_2 + P_2) + H_2 f'(H_2 + P_2) - C = 0 \quad (\text{A4})$$

Every parasitic egg gains its layer a net reward  $R_p$ , where

$$R_p = f(H_2 + P_2) - C \quad (\text{A5})$$

As the number of (host or parasite) eggs laid in a nest increases, competition effects mean that the value of a parasitic egg ( $R_p$ ) decreases. Hence, for any fixed number of host eggs  $H_2$ , we expect that parasites will continue laying whilst  $R_p$  is still positive. However at some point competition will mean that  $R_p$  falls below zero. We would not expect a parasite to lay such an egg, hence parasitism will stop just before  $R_p$  falls

below zero. For analytic convenience, we approximate the number of parasitic eggs laid by a continuous function. In this limit, the critical point occurs at the value when further parasitism would not be profitable, at exactly  $R_P=0$ , and so

$$f(H_2 + P_2) = \frac{C}{\gamma} \quad (\text{A6})$$

This simplification allows us to avoid the complications brought about by having to deal with whole numbers of eggs, but does not fundamentally change the nature of the model representation.

Combining (A4) & (A6) gives

$$H_2 f'(H_2 + P_2) = -\left(\frac{1}{\gamma} - 1\right)C \quad (\text{A7})$$

Note that parasitism may be possible, but the optimal worth of  $P_2$  may be zero, this occurs if (A4) and (A6) cannot be solved simultaneously, so that  $H_2 = H_1$  and

$$f(H_1) < \frac{C}{\gamma} \quad (\text{A8})$$

Now, equations (A3) and (A4) imply that

$$f(H_1) + H_1 f'(H_1) = C = f(H_2 + P_2) + H_2 f'(H_2 + P_2). \quad (\text{A9})$$

However, since  $f'(x) < 0$ ,

$$f(H_2 + P_2) + H_2 f'(H_2 + P_2) \geq f(H_2 + P_2) + (H_2 + P_2) f'(H_2 + P_2). \quad (\text{A10})$$

Together these mean that

$$f(H_1) + H_1 f'(H_1) \geq f(H_2 + P_2) + (H_2 + P_2) f'(H_2 + P_2). \quad (\text{A11})$$

Using condition (23), (A11) implies that

$$H_1 \leq H_2 + P_2 \quad (\text{A12})$$

This is the first important result of our analysis: parasitism never leads to a reduction in the total number of eggs in a nest, and can increase this total number. To explore the relative sizes of  $H_1$  and  $H_2$ , we need to select a specific functional form for  $f$ . If we assume that  $f(x)$  is described by a simple geometric decline:

$$f(x) = Ax^{-\alpha}, \quad (\text{A13})$$

where  $0 < \alpha < 1$ , then this fulfils conditions (2.1)-(2.3). Increasing  $\alpha$  causes the value of an egg to decrease more rapidly with increasing final clutch size. It is easy to show that

$$x \frac{df(x)}{dx} = x(-\alpha Ax^{-\alpha-1}) = -\alpha Ax^{-\alpha} = -\alpha f(x). \quad (\text{A14})$$

Making this substitution in equation (A3) gives

$$H_1 = \left( \frac{A(1-\alpha)}{C} \right)^{\frac{1}{\alpha}}. \quad (\text{A15})$$

In the case where parasitism is possible, we focus on the interesting situation where  $P_2 > 0$ . From (A6) we obtain

$$H_2 + P_2 = \left( \frac{A\gamma}{C} \right)^{\frac{1}{\alpha}} \quad (\text{A16})$$

and (A7) becomes

$$H_2 f'(H_2 + P_2) = H_2 (-\alpha A (H_2 + P_2)^{-\alpha-1}) = -\alpha A H_2 \left( \frac{A\gamma}{C} \right)^{-\left(\frac{\alpha+1}{\alpha}\right)} = -\left( \frac{1-\gamma}{\gamma} \right) C \quad (\text{A17})$$

This gives

$$H_2 = \left( \frac{1-\gamma}{\alpha} \right) \left( \frac{\gamma A}{C} \right)^{\frac{1}{\alpha}} \quad (\text{A18})$$

and

$$P_2 = \left(\frac{\gamma A}{C}\right)^{\frac{1}{\alpha}} - H_2 = \left(\frac{\gamma A}{C}\right)^{\frac{1}{\alpha}} \left(1 - \frac{1-\gamma}{\alpha}\right) \quad (\text{A19})$$

This is positive providing

$$\alpha > 1 - \gamma \Rightarrow \alpha + \gamma > 1 \quad (\text{A20})$$

Thus if condition (A20) is satisfied, we expect non-zero levels of parasitism. It is no surprise that increasing  $\gamma$  makes parasitism more attractive, since  $\gamma$  is the probability that a parasitically laid egg will be accepted by the nest-owner. Increasing  $\alpha$  increases the effect of increasing clutch size on the value of an egg. This benefits parasitism, since in the limiting case where  $\alpha = 0$ , the value of an egg is unaffected by final clutch size and so (providing  $\gamma < 1$ ), the ESS strategy is to lay all your eggs in your own nest. Notice that neither  $A$  (which scales the value of eggs) or  $C$  (their cost) has any influence on whether parasitism occurs. This is due to the fact that the rewards to both hosts and parasites are affected by these parameters in exactly the same way ( $A$  is a common factor in all rewards,  $C$  in all costs). Parasitism occurs if a parasite is willing to lay in a situation when a host is not, and whether this occurs or not does not depend upon  $A$  or  $C$ . Note that the number of parasitic eggs laid, if parasitism does occur, does depends upon these parameters through the ratio  $A/C$ .

In the situation where (A20) is satisfied, we can work out the ratio

$$\frac{H_2}{H_1} = \left(\frac{1-\gamma}{\alpha}\right) \left(\frac{\gamma}{1-\alpha}\right)^{\frac{1}{\alpha}} \quad (\text{A21})$$

This ratio is greater than unity, thus parasitism causes increased laying in a bird's own nest, provided that

$$\alpha^\alpha (1-\alpha) < \gamma(1-\gamma)^\alpha \quad (\text{A22})$$

Returning to the general form for the function  $f(x)$ , we investigate the robustness of our predictions to changing functional form. No parasitism occurs if (A3) and (A8) hold simultaneously. Since the solution of (A3) is independent of  $\gamma$ , there is no

parasitism for sufficiently small  $\gamma$ . Similarly, since  $f'(x) < 0$ , there is parasitism when  $\gamma$  is sufficiently close to 1, with  $H_1 > H_2$  ( $H_2=0$  when  $\gamma=1$ ). We now examine what happens at the point where  $\gamma$  becomes sufficiently large for parasitism to occur.

Dividing (12) through by  $H_2 + P_2 - H_1$  and rearranging gives

$$H_1 \frac{f'(H_2 + P_2) - f'(H_1)}{H_2 + P_2 - H_1} + \frac{H_2 - H_1}{H_2 + P_2 - H_1} f'(H_2 + P_2) = -\frac{f(H_2 + P_2) - f(H_1)}{H_2 + P_2 - H_1} \quad (\text{A23})$$

Consider a value of  $\gamma$  just larger than  $C/f(H_1)$  ( $f(H_1)=C/\gamma+\delta$ ); thus

$f(H_2 + P_2) - f(H_1) = -\delta$  and as  $\delta$  converges to 0,  $H_2 + P_2$  converges to  $H_1$ . Since we know that  $H_2 + P_2 - H_1 > 0$ , letting  $\delta$  tend to 0 in equation (A23) yields

$$H_1 f''(H_1) + \lim\left(\frac{H_2 - H_1}{H_2 + P_2 - H_1}\right) f'(H_1) = -f'(H_1) \quad (\text{A24})$$

Which in turn means that  $H_2 - H_1 > 0$  just after the point when parasitism starts if and only if

$$H_1 f''(H_1) + f'(H_1) > 0 \quad (\text{A25})$$

This may or may not occur for a particular value of  $C$ , but for any plausible function it must occur for some values of  $C$ . This is due to the fact that over the whole range of possible values of  $C$ , all positive values of  $H_1$  are a solution of (A3), due to inequalities (2.2) & (2.3), so for this not to occur for any  $C$  would require

$$\frac{d(xf'(x))}{dx} < 0 \quad (\text{A26})$$

for all positive values of  $x$ , which can only occur if  $f(x)$  becomes negative for some  $x$ , which is not possible.