

Parasites and supernormal manipulation

Øistein Haugsten Holen, Glenn-Peter Sætre†, Tore Slagsvold and Nils Chr. Stenseth*

Division of Zoology, Department of Biology, University of Oslo, PO Box 1050, Blindern, N-0316 Oslo, Norway

Social parasites may exploit their hosts by mimicking other organisms that the hosts normally benefit from investing in or responding to in some other way. Some parasites exaggerate key characters of the organisms they mimic, possibly in order to increase the response from the hosts. The huge gape and extreme begging intensity of the parasitic common cuckoo chick (*Cuculus canorus*) may be an example. In this paper, the evolutionary stability of manipulating hosts through exaggerated signals is analysed using game theory. Our model indicates that a parasite's signal intensity must be below a certain threshold in order to ensure acceptance and that this threshold depends directly on the rate of parasitism. The only evolutionarily stable strategy (ESS) combination is when hosts accept all signallers and parasites signal at their optimal signal intensity, which must be below the threshold. Supernormal manipulation by parasites is only evolutionarily stable under sufficiently low rates of parasitism. If the conditions for the ESS combination are not satisfied, rejector hosts can invade using signal intensity as a cue for identifying parasites. These qualitative predictions are discussed with respect to empirical evidence from parasitic mimicry systems that have been suggested to involve supernormal signalling, including evicting avian brood parasites and insect-mimicking *Ophrys* orchids.

Keywords: arms race; brood parasitism; evolutionarily stable strategy; mimicry; signal; supernormal stimuli

1. INTRODUCTION

Mimicry, as defined by Vane-Wright (1980), 'involves an organism (the mimic) which simulates signal properties of a second living organism (the model) which are perceived as signals of interest by a third living organism (the operator), such that the mimic gains in fitness as a result of the operator identifying it as an example of the model' (p. 4). Several social parasites use mimicry for exploiting their hosts. An example of such a parasitic mimic is the beetle *Atemeles pubicollis*, which parasitizes ants of the species *Formica polyctena* (Hölldobler & Wilson 1990). The beetle larvae reside inside the ant colony and use chemical signals for gaining acceptance. They show begging behaviour towards their hosts in a similar way to ant larvae. When touched by an ant, they seek contact with the ant's head and use their mouth parts for mechanically stimulating the ant's labium. The worker ants respond by regurgitating food to the beetle larvae.

If the intensity of the signal carries extra information about the model's quality or status, the operators may benefit from allocating more resources to high-intensity signalling model organisms. Some parasites exploit this. *Atemeles pubicollis* larvae beg more intensely than ant larvae and receive more food (Hölldobler & Wilson 1990).

A strictly increasing open-ended host response function (figure 1) may be a very simple rule of thumb that ensures a correct response to all signals in the models' normal signal intensity range. It may also explain how supernormal stimuli, i.e. strong signal intensities outside the

normal signal intensity range of the model organisms, lead to abnormally strong responses from the operator. In the 'insect orchids' of the genus *Ophrys*, the flowers mimic female wasps and bees through chemical, visual and tactile stimuli and thereby attract males, which try to copulate with the flowers, thus ensuring pollination (Kullenberg 1961; Proctor & Yeo 1973). Kullenberg (1961) found that *Ophrys* flowers presented supernormal olfactory stimuli and that male bees of two species in the genus *Andrena* preferred to descend on the orchid *Ophrys lutea* when given a choice between the flower and an immobilized female bee. Staddon (1975) and Ryan (1990) discussed how supernormal preferences can arise and gave several examples of open-ended response functions.

Chicks of the common cuckoo (*Cuculus canorus*) soon outgrow their host parents, have a large red gape and a very intense begging call and receive much more investment from the host parents than any ordinary host chick. Dawkins & Krebs (1979) suggested that the cuckoo chick uses supernormal stimuli for manipulating the host into accepting it and that the host can no more resist than 'the junkie can resist his fix' (p. 496). The parasite's exaggerated stimulus compensates for its imperfect mimicry of the model organism. Redondo (1993) built on this idea and presented a detailed proximate motivational model for explaining how exaggerated signals may help brood parasites secure acceptance.

The hypothesis that parasites manipulate hosts by using supernormal or exaggerated signals has received much attention. In this paper, we undertake a formal and strict examination of this hypothesis through game theory modelling. The central idea is that operators can use signal intensity as a cue for identifying parasitic mimics when the perceptual constraints of the operators prohibit recognition of mimics on the basis of other signal characteristics. The evolutionary consequences of such anti-parasite adaptations are examined.

* Author for correspondence (n.c.stenseth@bio.uio.no).

† Present address: Department of Evolutionary Biology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18d, SE-752 36 Uppsala, Sweden.

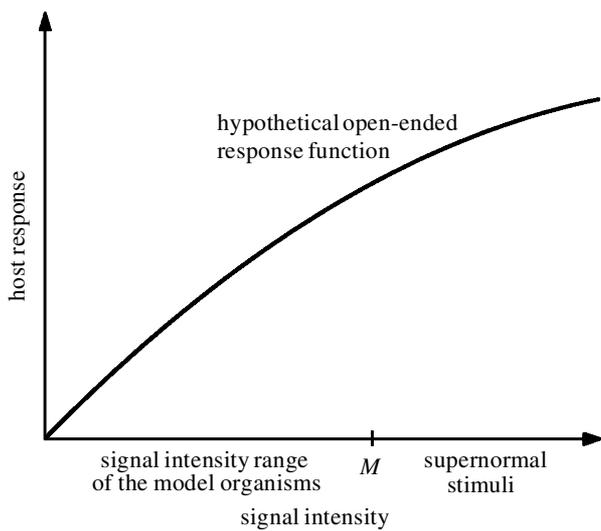


Figure 1. A model organism sends a signal that is recognized by the host (operator) organism, which then responds. The host has an open-ended response function and gives a stronger response to more intense signals. The model organisms have the signal intensity range $(0, M)$. No model organism is capable of sending a signal of intensity equal to or higher than M . Any signal of equal or higher intensity than M is a supernormal stimulus.

2. THE MODEL

We adopt Hammerstein's extended n -species game theoretical framework and the concept of evolutionarily stable strategy (ESS) combinations (as presented by Riechert & Hammerstein 1983). Assuming that the parasite and the host do not compete for resources in any other way than through the act of parasitism itself, we use the rate of parasitism, which is denoted by P , as an (indirect) measure of the relative species abundances (see table 1 for a summary of the notation). The rate of parasitism describes the probability that a signal detected by the host has been sent out by a parasitic mimic rather than by a model organism. Given a certain rate of parasitism, if the strategy I is an ESS in the population of the first species on condition that the population of the second species plays the strategy J , and the strategy J is an ESS in the population of the second species on condition that the population of the first species plays the strategy I , then the interspecific strategy combination (I, J) is an ESS combination (Riechert & Hammerstein 1983).

By convention, the term ESS is usually reserved for equilibrium strategies that are found when there is intraspecific frequency dependence (Maynard Smith 1982; Parker 1984; Parker & Maynard Smith 1990; Reeve & Dugatkin 1998). However, we will adopt Parker & Hammerstein's (1985) usage of the term ESS and let it include intraspecific frequency-independent equilibrium strategies in two-species games, which is justified for the reason that two-species games introduce interspecific frequency dependence.

(a) Strategies and fitness functions

Consider the host organism to be the operator and the parasitic organism to be the mimic. The signal of interest varies in intensity and carries extra information about the

quality or status of the model organism. No model organism is capable of sending a signal of intensity equal to or higher than some limit M . A naive host is assumed to respond actively to all the signals of interest it detects and to provide a stronger response to the more intense signals using an open-ended response function that has evolved in the absence of parasitism. We denote the naive host response strategy by h_N .

We will examine whether a rejector host may invade if parasitic mimics are introduced into the naive host population. A host playing a rejector strategy h_R is one that only responds to signals with intensities below h_R and ignores or rejects both model organisms and mimics presenting signals of intensity h_R or higher. The rejector threshold may take on any value, i.e. $h_R \in [0, \infty)$.

The cumulative function $F_R(h_R)$ gives the expected fitness gain to a rejector host playing h_R when it detects (and possibly responds to) a signal sent by a model organism (figure 2). If the signal sent by the model organism is ignored, the host's fitness gain is zero. We assume that $F_R(h_R)$ and the open-ended response function are the result of a signalling equilibrium between the host and the model organism and that they do not change.

The rejector adaptation carries a 'vigilance cost' V_C , which all rejector hosts must pay. It reflects physiological costs, such as spending extra energy watching out for parasitic mimics (i.e. assessing the signal intensities) and other costs, such as reduced fitness in other traits. In the absence of parasitism the expected change in fitness to a rejector host detecting a signal is $F_R(h_R) - V_C$. Naive hosts do not pay the cost V_C and their expected fitness gain is $F_N = F_R(M)$. Note that the cost of ignoring or rejecting high-intensity signalling model organisms is not included in V_C , but is dealt with explicitly through $F_R(h_R)$.

Assume that a parasitic mimic needs to present a signal at least as intense as some threshold T in order to trigger sufficiently strong responses from hosts to have any chance of surviving and later reproducing. A trade-off exists: more intense signals trigger stronger responses from the host, but also carry higher costs to the mimic (e.g. physiological costs or increased danger of predation). The constant Q denotes the optimal signal intensity of the parasites in a naive host population and $Q > T$. Note that T and Q are invariable evolutionary constraints and not part of any strategy. If T and Q are small, the parasites need only weak responses from the host. If T is very high, the parasites have very high needs. If T is much smaller than Q , the parasites can survive over a wide range of host responses.

The parasite strategies consist of sending signals at different intensities, which are denoted by p_s . The parasite may play any strategy $p_s \in [T, \infty)$. The parasite's expected gain in fitness when it plays against a naive host is strictly increasing for $p_s \in [T, Q]$ and strictly decreasing for $p_s > Q$.

The cost of responding to a parasitic mimic is denoted by C and is measured relative to the fitness value of ignoring the signal. The possible cost of wasting time on a parasite and, thus, missing out other signal encounters is included in C . Because the host has a strictly increasing, open-ended response function, it is realistic to assume that C increases with the signal intensity of the parasites. Physical exhaustion caused by a strong response to an intense signal may, for instance, decrease the host's

Table 1. Summary of the symbols used in the model.

(See the main text for complete explanations.)

notation	definition
hosts	
h_N	the naive host strategy
h_R	a rejector host strategy
s	the parasite signal intensity at which the rejector hosts that are playing $h_R = p_S$ and the naive hosts have equal fitness
$F_R(h_R)$	the expected fitness gain for a rejector host that detects (and possibly responds to) a signal from a model organism
$F_N = F_R(M)$	the expected fitness gain for a naive host that detects and responds to a signal from a model organism
V_C	the vigilance cost ($V_C = c \times F_N$)
$C(p_S)$	the cost of parasitism ($C(p_S) = (a + b \times p_S)F_N$)
parasites	
p_S	a parasite signalling strategy
Q	the optimal parasite signal intensity in a naive host population
T	the lowest parasite signal intensity that may trigger a sufficiently strong response from a host so as to give the parasite a chance to survive and later reproduce
others	
M	the upper bound of the model organism's signalling range ($0, M$): no model organism signals with intensity M or higher
P	the rate of parasitism
P'	the maximum rate of parasitism attained

survival and/or reduce its ability to respond in later signal encounters. We will use the strictly increasing linear function $C(p_S) = (a + b \times p_S)F_N$ for describing the cost of parasitism, where a scales the constant component of the cost of parasitism (e.g. wasting of valuable time) and b scales a varying component of the cost of parasitism (e.g. physical exhaustion causing reduced survival). However, the qualitative predictions would be the same for any strictly increasing function $C(p_S)$.

(b) Assuming a constant rate of parasitism

A mixed strategy cannot be an ESS if there is no intraspecific frequency dependence (Parker & Hammerstein 1985). As a result we will only need to look for pure ESSs in our analysis.

We first make the assumption that P is kept constant, which is useful for an initial analysis, but in general unrealistic; this assumption will be relaxed later. Thus, when a naive host responds to a signal under the risk of parasitism the expected pay-off is $(1 - P)F_N - PC$. If the parasitic mimics play the strategy p_S , which strategy should a host answer with? If the host plays a strategy $h_R > p_S$ it will respond to signals from possible parasites and may end up paying the cost C . The rejector host's expected pay-off will then be $(1 - P)F_R(h_R) - PC - V_C$. The strategy h_N yields a better pay-off than any rejector strategy $h_R > p_S$, because $(1 - P)F_N - PC > (1 - P)F_R(h_R) - PC - V_C$. Conversely, if the host plays $h_R \leq p_S$ it will avoid responding to the parasites' signals and its pay-off will be $(1 - P)F_R(h_R) - V_C$. The host strategy $h_R = p_S$ yields a better pay-off than all other rejector strategies that satisfy $h_R \leq p_S$ (an exception is when $p_S > M$, in which case any h_R that satisfies $M \leq h_R \leq p_S$ will be an equally good strategy).

In conclusion, the rejector strategy $h_R = p_S$ yields a higher pay-off than h_N when $(1 - P)F_R(p_S) - V_C > (1 - P)F_N - PC$. We then obtain the rejection criteria

$$C(p_S) > \frac{(1 - P)}{P}(F_N - F_R(p_S)) + \frac{V_C}{P}. \quad (2.1)$$

In general, the host should be more likely to reject intense signals when (i) the cost of parasitism (C) is high, (ii) responding to model organisms that signal with intensities equal to or higher than the parasites' signal intensity contributes little to the hosts' expected fitness (i.e. $F_N - F_R(p_S)$ is small), (iii) the rate of parasitism (P) is high, and (iv) the vigilance cost (V_C) is small.

Note that the rejection criteria (equation (2.1)) is always satisfied if $P > (F_N + V_C)/(F_N + aF_N)$, which is most easily seen by inserting $p_S = 0$ into the equation. In this special case, it is simply optimal for the host to ignore all signals, as the expected fitness gain of responding to any signal is negative. Without making additional assumptions about the life history and ecology of the two species, the biological relevance of this case is not clear. Thus, in the following we will merely assume that $P < (F_N + V_C)/(F_N + aF_N)$.

Assume that h_R^* is an ESS for the host population. No parasite strategy that satisfies $p_S \geq h_R^*$ can then be an ESS as all other parasite strategies would do just as well. Any parasite ESS must therefore satisfy $p_S < h_R^*$. However, all rejector host strategies $h_R^* > p_S$ yield a lesser pay-off than the naive host strategy h_N and, consequently, rejector host strategies cannot be part of any ESS combination.

Assume, instead, that the naive host strategy h_N is an ESS. This induces the parasite ESS $p_S^* = Q$. We can see from equation (2.1) that h_N will be the best response to p_S^* when Q is sufficiently low. The exact parasite signal intensity s at which the host is indifferent between rejecting and responding to a signaller may be found from solving

$$C(s) = \frac{(1 - P)}{P}(F_N - F_R(s)) + \frac{V_C}{P}. \quad (2.2)$$

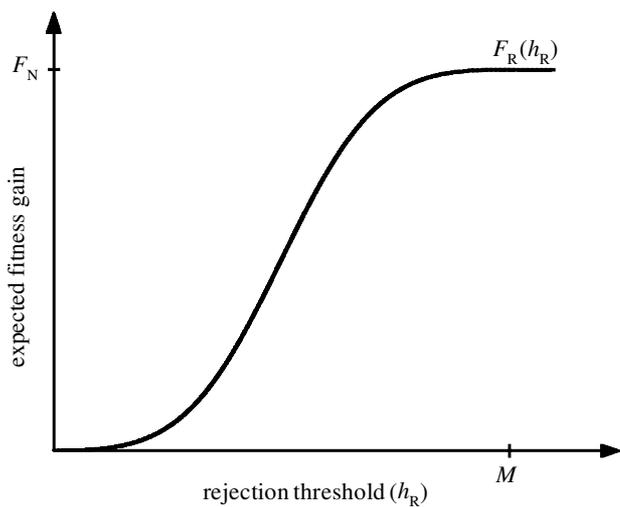


Figure 2. The function $F_R(h_R)$ describes the expected fitness gain to a host playing the rejector strategy h_R in an encounter with a signal sent by a model organism. We assume that both the probability distribution of the signal intensity of the model organisms and the hosts' expected fitness gain when responding to a signal are strictly positive in the signal intensity range $(0, M)$. This implies that the function $F_R(h_R)$ must be strictly increasing for $h_R \in [0, M]$. The function $F_R(h_R)$ must also be constant for all strategies $h_R > M$, because no model organism signals with intensities equal to or exceeding M . As long as these two conditions hold, the choice of $F_R(h_R)$ does not change the qualitative predictions. Signal intensities close to M are assumed to be rare among model organisms, thereby making the average cost of rejecting signals with such intensities low even if they signify model organisms of high value to the host. Most model organisms are assumed to have moderate signal intensities, and very low signal intensities are assumed to be rare. It is thus reasonable that $F_R(h_R)$ is S-shaped. The function $F_R(h_R)$ used here is the cumulative function of a modified normal distribution, which has first been terminated outside the third standard deviation on each side of the mean and lowered so that the endpoints touch the x -axis. $F_R(h_R)$ is approximated by polynomial fitting whenever graphs are plotted throughout the paper.

The strategy combination (h_N, p_S^*) is an ESS combination if $Q < s$. Naive hosts that accept all signalers, and naive parasites that signal at their optimal signal intensity Q , will then coexist in an evolutionary equilibrium. If $Q > s$, no ESS combination exists. The threshold s increases when the rate of parasitism P decreases (equation (2.2)), thereby allowing parasites with higher demands (high Q) to also coexist stably with hosts.

(c) *Relaxing the assumption of a constant rate of parasitism*

Let us relax the assumption of a constant rate of parasitism P and instead make the more realistic assumption that the rate of parasitism is always below some constant P' . The rate of parasitism may be kept below P' through many mechanisms, such as density-dependent factors reducing the population size of parasites, predation and territorial behaviour among parasites. Equation (2.2) may be rearranged to

$$P = \frac{V_C + F_N - F_R(s)}{C(s) + F_N - F_R(s)}. \quad (2.3)$$

We use equation (2.3) for plotting s as a function of P for a range of different parameter values in figure 3. Figure 3 has the following interpretation. Given a maximum rate of parasitism P' , the strategy combination $(h_N, p_S^* = Q)$ is an ESS combination if the point (P', Q) is to the left of the curve $s(P)$. The range of values for (P', Q) that gives rise to this ESS combination increases with the vigilance cost (the curve $s(P)$ moves to the right) (see figure 3c) and decreases with an increasing cost of parasitism (the curve $s(P)$ moves to the left) (see figure 3a,b). (Note that the area to the right of where $s(P)$ intersects the x -axis corresponds to the special case when $P > (F_N + V_C)/(F_N + aF_N)$, in which the hosts do best by ignoring all signals.)

The qualitative predictions of the model are robust regarding the choice of parameter values. We find that parasites with high signal intensity optima will enjoy a stable coexistence with naive hosts if the maximum attained rate of parasitism is sufficiently low. This makes good sense because the vigilance cost V_C is always paid by rejectors, whereas the cost of parasitism $C(p_S)$ is only paid by naive hosts with a probability equal to the rate of parasitism. The parasites may even use supernormal stimuli for maximizing host responses at sufficiently low rates of parasitism without running any risk of rejection. If the maximum attained rate of parasitism is high, a parasite with a relatively low optimal signal intensity may still safely 'hide' among model organisms, as the cost of rejecting model organisms along with the parasites will be too high.

(d) *Unstable dynamics*

The mimicry system is evolutionarily unstable if the rate of parasitism is high or $Q > s(P')$. This is when the point (P', Q) is to the right of the curve $s(P)$ in figure 3. Although the model makes no prediction about the evolutionary and ecological consequences of this instability, an informal analysis may provide some insight.

First, let us assume a constant P and that $Q > s(P)$. Parasites that play $p_S^* = Q$ invade a naive host population and, in the beginning, they thrive because the hosts lack counter-defences. However, after some time a mutant host strategy h_R that satisfies $s < h_R \leq p_S^*$ may arise. This strategy will have higher fitness against parasites playing p_S^* than the naive host strategy h_N . When the frequency of the strategy h_R increases in the host population, the expected fitness of parasites playing p_S^* will decrease. The parasites playing p_S^* may be invaded by mutant parasite strategists playing $p_S < h_R$, which do not signal at their optimum, but are not rejected. This may select for hosts with rejection thresholds less than h_R , which again may select for even lower parasite signalling intensities and so on. A race towards lower parasite signalling intensities and host rejection thresholds will result. If $T < s$ the race may end when the parasites' signal intensities are so low ($p_S < s$) that naive hosts will reinvade, thereby paving the way for parasites playing $p_S^* = Q$ and initiating a new race. Alternatively, if $T > s$, the race may end when all parasites are routinely rejected and no mutant parasites with even lower signal intensities can survive (when $h_R \leq p_S = T$). At this point, all parasite strategies yield zero in pay-off, and any parasite strategy could in theory invade due to random drift and destabilize the situation again.

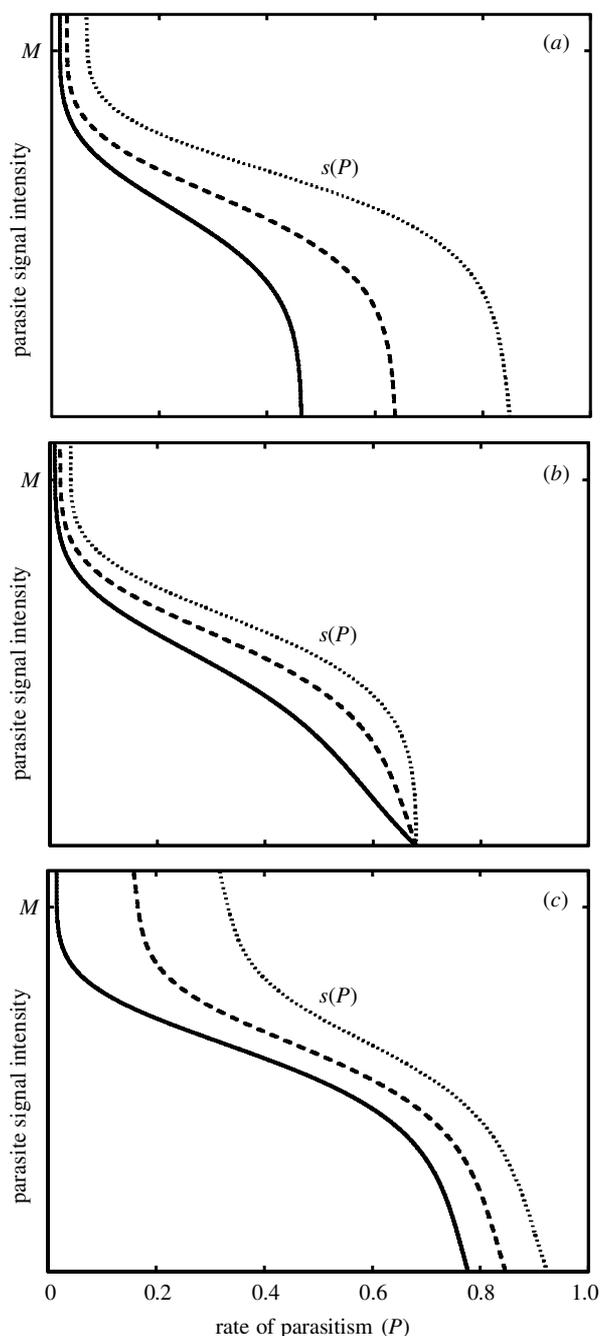


Figure 3. The threshold value s is the parasite signal intensity at which the host is indifferent between accepting and rejecting parasites. Each figure shows the threshold s as a function of the rate of parasitism P for three different choices of parameters. The parasite signal intensity is denoted by p_S . If the point (P, p_S) is to the left of $s(P)$ then the host maximizes its pay-off by playing the naive strategy h_N . If the point (P, p_S) is to the right of $s(P)$ then the host maximizes its pay-off by playing the rejector strategy $h_R = p_S$. If (P, p_S) is lying on $s(P)$ then h_N and $h_R = p_S$ yield equal pay-offs. The optimal signal intensity of the parasites in a naive host population is denoted by Q and the maximum attained rate of parasitism is denoted by P' . If the point (P', Q) is to the left of $s(P)$ the strategy combination $(h_N, p_S^* = Q)$ is an ESS combination. See the main text for further explanation. We have chosen the following parameter values, using $C(p_S) = (a + bp_S)F_N$ and $V_C = cF_N$. (a) $b = 0.1$ and $c = 0.02$. Solid line, $a = 1.2$; dashed line, $a = 0.6$; dotted line, $a = 0.2$. (b) $a = 0.5$ and $c = 0.02$. Solid line, $b = 1.5$; dashed line, $b = 0.5$; dotted line, $b = 0.01$. (c) $a = 0.3$ and $b = 0.3$. Solid line, $c = 0.01$; dashed line, $c = 0.1$; dotted line, $c = 0.2$.

If we relax the assumption of a constant rate of parasitism, the rate of parasitism will depend on the pay-off functions of the hosts and parasites. An initial high rate of parasitism may select for rejector hosts and cause a race towards lower parasite signalling intensities and host rejection thresholds, as explained above. The further the signal intensities of the parasites decrease below Q , the less success the parasites will have and the rate of parasitism may decrease. This may cause naive hosts to reinvade again, thereby paving the way for parasites playing at their optimal signal intensity p_S^* . If the parasites are obligate supernormal manipulators (i.e. $T > M$) and the vigilance cost is very small, it may take a long time before naive hosts reinvade and, in the meantime, the parasites may become extinct. If $T < M$ or the vigilance costs are substantial, naive hosts may reinvade more rapidly.

Although an informal analysis surely is useful, we should not forget that several complicating factors are left out. For instance, as rejector hosts have less success than unparasitized naive hosts, the population size of the hosts may decrease when rejection is widespread, which again may influence the rate of parasitism. It would be interesting to do a more formal examination of the evolutionary and ecological dynamics of this game, but a suitable theoretical framework is unavailable at present. However, we may deduce one very important prediction from the model. If the system is not in an evolutionarily stable state (i.e. if no ESS combination exists), at least a part of the host population is expected to reject both model organisms and parasites that signal with high intensity.

(e) Limitations of the model

We have assumed that the hosts have a perfect assessment of the signal intensity at the point of decision. In reality, there will be assessment errors and the hosts may erroneously accept some signallers with high signal intensities and reject others with low signal intensities. If we assume that the host's assessment errors do not influence which strategy is optimal for the parasite, then imperfect assessment will only decrease the fitness of rejectors, as naive hosts do not have to assess whether the signal intensity is above or below any threshold. Hence, the ESS combination will exist for a broader range of values of P' and Q . If the cost of the assessment errors is constant, it will yield the same results as for the cost V_C (see figure 3c). However, without actually developing a new model, it is difficult to evaluate the influence of assessment errors on the parasite's choice of strategy. In order to do this, we may need to obtain the probability distribution of the assessment errors and the explicit fitness functions of both hosts and parasites.

We have assumed frequency independence in the host population with respect to rejection strategies. In the case of evicting brood parasites, both the male and female in a host pair feed the parasite. Thus, one could imagine conflicts of interest between the host parents in this system. If rejector strategies are adaptive and most individuals in the host population are rejectors, naive hosts may have the highest fitness, because they can let their partners pay the vigilance costs, but enjoy all the benefits of rejection themselves with a high probability. A

preliminary analysis (O. H. Holen, unpublished data), which depends on the assumption of perfect signal assessment, shows that no new ESS combinations arise even when such frequency dependence is introduced into the host population. The assumption of frequency independence in the host population would hold if chicks were rejected only by females. Observational data support the suggestion that only females reject eggs in some species (Palomino *et al.* 1998). Note that relaxing the assumption of frequency independence has little consequence when rejection is found to be maladaptive, as in the ESS combination we identified.

We have assumed that C , V_C and $F_R(h_R)$ are identical for all hosts, and that T and Q are identical for all parasites. However, these may vary depending on the age, sex or status of the individual. The model organisms may also be under strong selection pressures to lower their signal intensities if the hosts are rejectors and may in fact adopt different strategies under different equilibria.

We have also assumed a strictly increasing open-ended response function. Natural selection may change the response function of the host under influence from parasites. This may have profound consequences. For instance, if the parasites were dependent on receiving more investment than any model organism, they would be very vulnerable to mutant hosts with response functions that do not increase for signal intensities above M .

3. DISCUSSION

If parasitic mimics can be recognized on the basis of their signal intensity, selection may favour parasites signalling with intensities close to those of the model organisms. Such parasites could 'hide' among model organisms, making effective rejector strategies with low rejection thresholds too costly, as they would cause the rejection of too many model organisms. According to our model, a parasite's signal intensity must be below a certain threshold in order to ensure acceptance and this threshold depends directly on the rate of parasitism. Rare parasites may use high signal intensities under ecological circumstances where more common parasites would be forced to use low signal intensities. The only ESS combination in the model is when hosts accept all signallers and parasites signal at their optimal signal intensity (Q), which must be below the threshold. Parasitic use of supernormal stimuli may be evolutionarily stable if the rates of parasitism are low, particularly if the host's vigilance costs are substantial. If the rate of parasitism or the optimal parasite signal intensity is too high, the conditions for the ESS combination are not satisfied and rejector hosts will invade.

In order to carry out a quantitative test of the model, we would need estimates for $F_R(h_R)$, $C(p_S)$, P' , V_C , Q and M . However, such detailed data are not yet available. Nevertheless, the robust qualitative predictions of the model may still provide clues to a better understanding of different mimicry systems.

In the case of the beetle *A. pubicollis*, we do not know whether the beetle larvae use supernormal stimuli for receiving food or whether they just pose as normal but very hungry ant larvae. It may be difficult to estimate the cost of parasitism, as, in addition to soliciting food from

host ants, the beetle larvae also prey on their hosts' larvae. Matters are further complicated by the beetle larvae's cannibalistic behaviour, which limits their numbers in each colony (Hölldobler & Wilson 1990).

Ophrys orchids mimic female bees and wasps in order to attract the males as pollinators. Kullenberg (1961) found that male bees of two *Andrena* species prefer mimicking orchids to real female bees and that *Ophrys* orchids present supernormal olfactory stimuli. Although the males receive no reward from the flowers (Wickler 1968), the cost of parasitism (i.e. the cost of pollinating a flower) is presumably very low, consisting mainly of the loss of some time and energy. There seem to be no costs associated with the loss of sperm, as no male ejaculate has been found on the flowers (Wickler 1968). The low cost of parasitism may delay or hinder the evolution of possible counteradaptations.

The *Ophrys* mimicry system raises an important question about supernormal preferences. Does the male prefer the orchid because it assesses it to be of higher quality than an ordinary female or is the flower just easier to detect? In the latter case, the bee would not necessarily be able to assess the intensity of the signal at all and it might be impossible to reject signals of high intensity. The proximate mechanisms behind the supernormal preference would differ in the two cases and our model only applies to the former.

In the case of evicting avian brood parasites, it seems sensible to assume that the host parents would assess begging over some period of time before deciding to reject or not in order to obtain a better estimate of the signal intensity. However, cognitive processes need not be directly responsible for rejection behaviour, because rejection could instead be triggered indirectly through physiological thresholds affected by the strength of the hosts' own responses to the signal, e.g. exhaustion.

In Europe, the common cuckoo usually parasitizes less than 5% of host nests (Rothstein & Robinson 1998). Host rejection of parasite eggs (e.g. Davies & Brooke 1988, 1998) may lower the effective rate of parasitism at hatching even further. As Lotem (1993) pointed out, if the host brood cannot be saved by rejection of the parasitic chick, then the cost of parasitism (which is equal to the 'benefit of rejection') is probably never greater than the reproductive value of unparasitized nests because re-nesting is not always possible and later nests usually have lower reproductive success. Under these circumstances, it is quite possible that cuckoo use of supernormal begging is stable.

Dawkins & Krebs (1979) and Redondo (1993) proposed that brood parasites might use supernormal or exaggerated stimuli for manipulating hosts into accepting them; we will refer to this as the 'manipulative exaggeration hypothesis'. The presence of supernormal stimuli may also be explained in other ways. For instance, if the host has an open-ended response function, exaggerated begging may merely help a parasite with very high needs to attract sufficient investment. Although it may benefit model organisms to moderate their signal intensity in order to maximize their inclusive fitness through the operator, parasitic mimics have no such interest and should be expected to be greedier.

According to the manipulative exaggeration hypothesis, the extra begging effort of the parasites is aimed at

securing acceptance. However, if the parasites were not seen as alien, they would benefit from lowering their begging intensity, thereby reducing the costs that are associated with exaggerated begging. Because rejection of alien-looking chicks is very likely to carry vigilance costs and misidentification costs (hosts may reject some of their own chicks), rejector genes will be selected against if no cuckoo chicks are ever rejected successfully. If rejection genes are rare, cuckoos signalling at a moderate (and optimal) intensity will be able to invade a population of signal-exaggerating cuckoos, which have to spend extra energy on begging. Redondo (1993) proposed that parasites with exaggerated signals might still persist, as the costs of the exaggerated signals may be largely paid for by the increased investment from the host parents. However, we cannot see how this could pay for the possible important extrinsic costs associated with exaggerated signalling, such as increased nest predation and reduced parental survival until chick independence. Moreover, the host response function may also be under selection, thereby reducing the response given to the most intense signallers. Hence, we suggest that the manipulative exaggeration hypothesis cannot explain exaggerated parasitic begging if no parasites are ever rejected.

No hosts are known to reject common cuckoo nestlings (Davies & Brooke 1988, 1998; Rothstein 1990). According to Kilner *et al.* (1999), the common cuckoo exploits the evolved chick-feeding rules of reed warbler hosts, exaggerating its vocalizations in order to compensate for its single gape. When comparing the begging and provisioning of cuckoo chicks to reed warbler broods, Kilner & Davies (1999) found no indications that the common cuckoo chick increases its vocalizations in order to counter host rejection behaviour.

To our knowledge, no host species is in fact known to reject parasitic nestlings. This lack of rejection can be reconciled with the evicting brood parasites' extreme begging in several ways. One possibility is that the typical rates of parasitism are sufficiently low so as to make supernormal or exaggerated begging evolutionarily stable. In this case, the exaggerated begging would simply serve to attract an optimal amount of investment from the hosts.

Another explanation is that the parasitic begging is only seemingly supernormal. It has been suggested that some components of chick begging signals (e.g. call rates) determine the total amount of food the parents bring to the whole brood and that other components of the signals (e.g. postures) determine how food is distributed to the nestlings (Kacelnik *et al.* 1995; Davies *et al.* 1998; Lotem 1998). Evicting brood parasites are reared alone in the nest and must ensure that the host parents bring enough food all by themselves. Thus, as Kilner & Davies (1999) pointed out, it is more meaningful to compare the cuckoo's begging display with the display of a whole brood than a single host chick, because the parasite faces the same problems as whole broods do when it tries to attract investment. Can it be that evicting parasitic nestlings exploits host-feeding rules that apply to whole broods and not to individual chicks? According to Davies *et al.* (1998), the common cuckoo chick mimics a whole brood with its begging calls. If parasites mimic broods and hosts respond to the combined begging from broods, the

parasite's begging intensity should be regarded as supernormal only if it is outside the normal begging intensity range of whole host broods. However, this is not necessarily the case. Reed warblers feed a cuckoo chick at approximately the same rate as four reed warbler chicks, which is the modal brood size in this species (Kilner *et al.* 1999). Other comparisons of the amount of food given to evicting brood parasite chicks and to whole host broods are also consistent with the idea that the parasites pose as normal host broods (Khayutin *et al.* 1982; Brooke & Davies 1989; Grim & Honza 1997; Gill 1998).

Whereas Dawkins & Krebs (1979) and Redondo (1993) assumed that an exaggerated signal may compensate for bad mimicry, we have started out with almost the opposite assumption, namely that the signal intensity is a cue like any other cue, which the host may in fact use for identifying parasites with otherwise good mimicry. An arms race between a parasite and a host may start out as the manipulative exaggeration hypothesis predicts, but if parasites are common it seems unlikely that acceptance can be secured in the long run by just increasing signal intensity.

The phenomenon of supernormal manipulation is certainly not yet fully understood. More empirical studies are needed in order to investigate host response functions and the signal intensity ranges of model organisms in detail. The fact that some hosts on average prefer or favour parasites to model organisms does not necessarily imply supernormality: the parasites may merely pose as high-quality (but perfectly normal) model organisms. It is also important to look further into the proximate mechanisms that give rise to the host preferences, particularly as they may affect the evolutionary stability of supernormal manipulation. Finally, the development of game theory models incorporating population dynamics could provide further insight into parasite–host arms races and into whether evolutionarily unstable situations may lead to extinctions or not.

We thank Steinar Engen for valuable comments on the manuscript and Hildegunn Viljugrein for helpful discussions. Financial support was provided by the S. G. Sønneland Foundation (to O.H.H.) and the Norwegian Research Council (to G.P.S.).

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