

Are Unusually Colored Eggs a Signal to Potential Conspecific Brood Parasites?

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ABSTRACT: It has previously been suggested that some species of birds make the last egg in their clutch pale as a signal to potential conspecific brood parasites that incubation has commenced. Here, we use game theory to show that the signaling function of pale eggs can be evolutionarily stable and resistant to cheating and to demonstrate that such a signal can only be maintained under strict conditions. The key conditions are, first, that there is a cost associated with the production of pale eggs (in particular, the cost of a pale egg produced early in the clutch must be more expensive than the cost of one produced later in the clutch) and, second, that the cost of making the last egg pale is not too great (relative to the costs of parasitism). We discuss the likelihood of these conditions being met in real systems and suggest empirical tests that would differentiate this theory from alternative nonadaptive explanations for pale eggs.

Keywords: evolution of honest signals, egg dumping, parasitism, host-parasite systems.

There have been many reports that the last laid egg of a sparrow clutch is generally considerably lighter in color than the other eggs (house sparrow *Passer domesticus*: Witherby et al. 1948; Lowther 1988; tree sparrow *Passer montanus*: Seebohm 1896; Seel 1968; grey-head sparrow *Passer griseus*: Bannerman 1953; Macworth-Praed and Grant 1953; Dead Sea sparrow *Passer moabiticus*: Yom-Tov 1980a). This has also been observed in other species (common tern *Sterna hirundo*: Gemperle and Preston 1955; Gochfield 1977; field-

fare *Turdus pilaris*: Håland 1986; herring gull *Larus argentatus*: Baerends and Hogan-Warburg 1982; moorhen *Gallinula chloropus*: McRae and Burke 1996).

There are several explanations for this effect (see "Discussion"), but Yom-Tov (1980a, 1980b) made the intriguing suggestion that this odd last egg might have evolved as a signal to potential brood parasites that the female has finished laying the clutch and has begun incubation. If a parasite lays its egg after incubation has commenced, then it would be unlikely to hatch, hence the potential parasite would benefit from heeding such a warning signal, if it could then find an alternative host nest where incubation had yet to commence. The signaling host would also benefit from avoiding the costs of warming an extra egg for some of the incubation period, costs that can be considerable (Monaghan and Nager 1997), as well as the possible cost of having to rear an extra chick. Hence, Yom-Tov considered this signal to be a likely explanation of the function of the pale last egg, although he did not consider any evolutionary aspects of the development and maintenance of such a signal. Our primary purpose is to identify the conditions necessary for the evolution and maintenance of such a signal and, hence, to evaluate whether this signaling mechanism is theoretically viable in any natural system.

Model

We assume that each bird in a population of potential host birds can play one of the following three strategies: According to the first, which we call "honest signaling" (*H*), the host bird's last egg is pale; according to the second, "cheating" (*C*), the host bird's first egg is pale; and according to the third, "nonsignaling" (*N*), none of the host bird's eggs are pale. We also assume that potential parasites can play one of two strategies: According to the first, which we call the first "receptive" (*R*), parasites sample nests at random until they find one with no pale eggs and then lay their eggs in this nest; and according the second, "ignoring" (*I*), parasites always lay eggs in the first nest encountered.

Furthermore, we assume that parasites act in a short time interval, after all hosts have started laying but when only a

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fraction t of host birds have a completed clutch. We define h as the total number of parasites divided by the total number of hosts. Hosts that cheat always have a signal egg in their nest, and thus they are immune to attack from parasites that respond to this signal. We assume that there is an extra cost associated with laying a signal egg and that this cost is dependent on the position of the egg in the clutch. Specifically, we assume that making the last laid egg pale costs E_2 and that making the first laid egg pale costs E_1 . The value of an unparasitized nest is V . This is reduced by C_1 for every parasitic egg laid in the nest before incubation begins and by C_2 for every parasitic egg laid after incubation begins. In addition, we assume that $C_1 > C_2$.

For simplicity, we assume that each parasite lays only a single egg. A parasite that lays its egg after incubation has begun in the host nest receives no reward. This is a simplification; its expected reward would, in reality, decline with the time elapsed since the last egg was laid, tending to zero quickly. If it lays in a nest before incubation starts, then its reward is modulated by the investment required to find and evaluate potential host nests. Thus, the net reward of laying in a nest before incubation starts is $Dg(i)$, where $D > 0$, i is the number of host nests considered by the parasite before it decides to lay ($i \geq 1$), and $g(i)$ is some decreasing function of i with $g(1) = 1$. For simplicity, we pick $g(i) = q^{i-1}$, where $0 < q < 1$, although our results are insensitive to the exact formulation of $g(i)$, providing that it decreases with i and tends to zero as i becomes very large.

We define the fractions of hosts playing strategies C , H , and N as s_1 , s_2 , and s_3 , respectively, such that

$$s_1 + s_2 + s_3 = 1.$$

The proportions of parasites playing R and I are p and $1 - p$, respectively. For consistency, we must have $ph \leq 1 - t$.

Model Predictions

We wish to look for evolutionarily stable states (ESSs), that is, situations in which no host or parasite could improve its net-gain rate by unilaterally switching to another strategy. We confine the details of our search for these ESSs to the appendix and summarize the results in figure 1. For some combinations of parameter values, no ESS exists. In such cases, providing that all the strategies are strictly heritable, it is likely that the system will undergo continuous cyclic change in relative frequencies of the different strategies, and this is indeed the case for our system (discussed later in this section). For other parameter values, we find that there are two different ESS situations. According to one, all hosts signal honestly by making their last egg pale

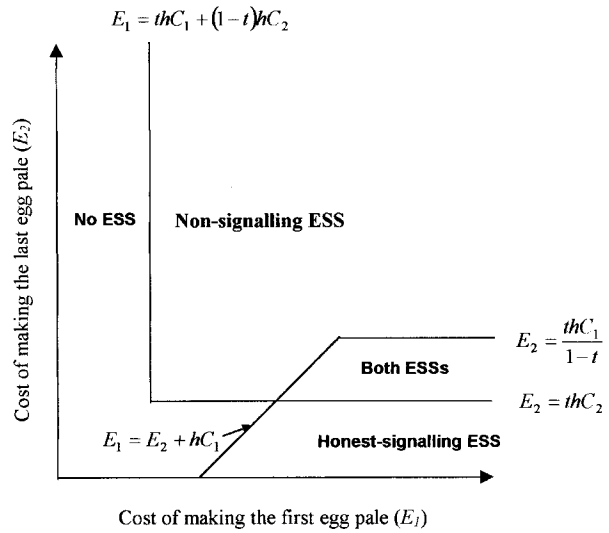


Figure 1: The potential evolutionarily stable states of the system as a function of the parameter values.

and all parasites are receptive to that signal; this is precisely the situation discussed by Yom-Tov (1980a, 1980b) and the most important prediction of our model. According to the other, none of the hosts produces a signal egg, and thus both parasite strategies produce identical behaviors and net rewards. In situations in which parameter values are such that both ESSs exist, the one that a given system settles on depends on the history of the system.

In order to obtain the ESS in which all hosts signal honestly, the parameter values must satisfy the following two conditions:

$$E_2 < \frac{thC_2}{1-t},$$

$$E_1 > E_2 + hC_1.$$

The first of these is easy to interpret. Each honest-signaler pays a cost E_2 in making their last egg pale; the benefit they get from this is that they avoid the risk of parasites laying eggs in their nests after they have completed their clutch with the signal egg. When all the hosts are signaling honestly and all the parasites are responding to that signal, then an individual that does not signal will not incur E_2 but will pay an expected cost of $thC_2/(1-t)$ from incubating parasitic eggs laid after clutch completion (eq. [A14]). Hence, satisfying the first of the conditions above ensures that, when all hosts are signaling honestly, any individual that switches to non-signaling will do worse than the rest. If the parameter values are such that the system

fails to satisfy this condition, then nonsignaling individuals can invade the population of honest signalers. Furthermore, we show in equation (A17) that, in this case, the net-reward rate of nonsignalers compared to honest signalers increases as their number in the population increases. This is not surprising since it is still evolutionarily stable for parasites to continue to be receptive to the signal because the signal is still honest when it appears and because reducing the fraction of signalers reduces the chance that any nonsignaler might be selected by a parasite. This occurs since fewer parasites reject the first nest they select because they find a signal egg in it. Hence, the population switches over entirely to nonsignaling. As figure 1 illustrates, this will be an ESS if the cost of producing a dishonest signal E_1 is sufficiently high that cheats do not invade (discussed later in this section).

If the system fails to satisfy the second of these conditions, then an individual that switches to cheating does better than the rest of the honest-signaling population (eq. [A13]). Hence, cheats begin to invade the population. This, in turn, causes the ESS for parasites to switch to ignoring signal eggs. The increase in nonreceptiveness in parasites reduces the effectiveness of cheating, which arrests their invasion and makes nonsignaling the most profitable option. Hence, both cheats and honest signalers do better by switching to nonsignaling. This switching continues until all of the host population stops signaling. Figure 1 shows that there are, once again, two possible outcomes. If no individual benefits from switching to honest signaling, then the system remains at an ESS with no hosts signaling. If, however, the reduction in the frequency of cheating means that honest signaling can invade, then this strategy sweeps through the population, and the system reverts to its original state, which was dominated by honest signaling. We have just argued that this population can be invaded by cheats, and so the cycle described above begins again. In summary, we have a situation in which there is no ESS. Instead, the system cycles through various phases: first honest signalers dominate, then there is a mixture of honest signalers and cheats, then nonsignalers dominate, then honest signalers dominate once again, and so on.

As discussed above, there is another ESS, one in which all hosts play the nonsignaling strategy. We can obtain this ESS providing that the following two conditions are satisfied:

$$E_1 > h(1 - t)C_1 + htC_2,$$

$$E_2 > thC_2.$$

If the system fails to satisfy the first of these, then an individual that switches to cheating does better than the

rest of the nonsignaling population, hence the strategy of cheating begins to spread in the population (eq. [A16]). When all hosts were nonsignaling there was no selection pressure on parasite strategy because parasites never encountered signal eggs. However, once cheats have invaded, there is very strong selection pressure on parasites to ignore signal eggs (since the signal is always dishonest). Hence, parasites switch to ignoring signals. When this occurs, the cheating signalers are disfavored, and the system returns to a situation in which individuals do not signal. Providing all parasites play the strategy that ignores signals, then the cheats cannot invade. Furthermore, there is now no selection pressure on parasite strategy (since signals are never encountered). Hence, if passive drift allows sufficient parasites to switch to the receptive strategy, then cheats can invade the population for a short time again. In this sense, there is no stable ESS, although we would expect that the system would spend the overwhelming majority of time at the configuration in which all individuals do not signal. Furthermore, any cost (no matter how small) that R parasites pay for looking for pale eggs would prevent such individuals from drifting into the population of I strategists.

If the system fails to satisfy the second condition, then honest signalers can invade the population of nonsignalers (eq. [A15]). As discussed above, if the cost of cheating E_1 is high, it will lead to an ESS solution in which all the hosts signal honestly. If the costs of cheating are low, then we obtain the situation described above in which there is no ESS. Instead, we get a cycle of invasions by honest signalers, then cheats, and then nonsignalers.

The last thing to notice about figure 1 is that, for a range of parameter values, both ESS solutions are possible simultaneously. In this situation, the system can settle to either of these situations (either with all hosts not signaling or all hosts signaling honestly), but the one reached will depend on the starting conditions of the system. Since it is most likely that natural systems evolved from a nonsignaling state, we would expect that the nonsignaling ESS is likely to be the most ecologically relevant in situations in which both are possible. The difficulty in reaching a signaling ESS in a system in which nonsignaling is both ancestral and an ESS is discussed in detail by Rodriguez-Girones (1999 and references therein).

Discussion

Our purpose in this article was to evaluate whether the theory that pale eggs could be a signal of clutch completion to brood parasites was internally consistent. Specifically, we sought to understand whether such a signal could ever evolve and remain resistant to the evolution of cheats. Our conclusion is that such resistance to cheating over evolutionary time is possible but only under certain condi-

tions. In no way does this conclusion mean that this candidate explanation for the observation of pale eggs is more likely than other potential explanations. All it means is that this explanation is at least theoretically possible and, as such, warrants further consideration alongside these other explanations.

Here, we have shown that a signaling function of pale eggs can be evolutionarily stable and resistant to cheating but that such a signal can only be maintained under strict conditions. The key assumptions are that the production of pale eggs induces a cost, which is greater if a pale egg is produced early in the clutch than it is if a pale egg is produced later in the clutch, and that the cost of making the last egg pale is not too great (relative to the costs of parasitism). The necessity of these assumptions makes intuitive sense. It is well established that signals must generally be costly in some sense in order to discourage cheating (Johnstone 1997). Similarly, if the signal is too expensive to produce, then individuals will do better by dispensing with it and paying the lesser costs of not signaling. Finally, if the costs of cheating were not greater than the costs of signaling in a situation in which all hosts are signaling honestly and all parasites are responding to the signal, then cheats will invade the system. Although these results are intuitive for signaling systems in general, we must also consider how valid they are for the specific signal of pale- or otherwise different-colored eggs. It seems likely that there is some adaptive value to the characteristic patterning of eggs of a given species, for example, for thermoregulatory reasons or as camouflage against predators (Brooke and Birkhead 1991) and, hence, that deviating from this patterning is costly to the parents' fitness. Hence, it seems reasonable that the first assumption is met. The second assumption may also be reasonable. Generally, the earlier an egg is laid in a clutch, the higher its chance of producing a viable chick (often because the female's reserves for egg production declines throughout the laying sequence). Hence, earlier laid eggs may be more valuable to the female than those laid later in the sequence, and thus impairing their performance with odd coloration might be more expensive. Although plausible, this hypothesis is in clear need of empirical testing. If such an effect is found, we can then test whether the second of the two conditions discussed on page 2 is satisfied. Similar experiments could also measure the costs of pale-egg production in comparison to those of parasitism in order to test the last of the three conditions discussed above. If pale eggs are more conspicuous to predators when the nest is unattended before incubation begins, then laying a pale egg early in the clutch might increase the risk of a predator discovering the nest. Again, this alternative pathway for an added cost to laying an early pale egg is amenable to experimental testing. However, obtaining such measure-

ments for even a single species would be difficult, and effective testing of the theory would require comparison of these values for a variety of species.

Before such detailed, large-scale experiments are attempted, we should empirically test the underlying basis of this mechanism, namely, that parasites are less likely to lay eggs in host nests containing pale eggs. Such experiments would have to control carefully for other factors that parasites might use to judge whether or not incubation had started, such as the number and temperature of the eggs or the behavior of the parents. Such experiments should be possible by clutch manipulations in a suitable study species. If we find no evidence that parasites use information from egg color (or, more generally, appearance), then further investigation of this theory in that population would be redundant.

Although the outstanding need is for further empirical work to test fundamental assumptions of the signaling mechanism, there is also scope for further model development. For example, one could consider parasites that can lay more than one egg or that use other cues (such as clutch size) in order to decide whether a clutch has been completed or not. Similarly, more complicated strategies could also be considered. The model simplifies reality by allowing no limit to the number of nests that a parasite can sample. In reality, once an egg is in the oviduct, it must be laid within a restricted time interval. Hence, it might sometimes be profitable for a parasite to lay its egg in a nest where incubation has already begun because the very slim chance of the egg producing a viable chick in this nest is better than the zero probability associated with failing to find a host nest in time and dropping the egg on the ground.

Our model predicts that cheating does not form part of any ESS. This conclusion is based on the assumption that all strategies are strictly heritable. Alternatively, if parasites are able to switch tactics on a very short time scale, so as to always adopt the tactic that maximizes their fitness, then a persistent mixture of honest signalers and cheats is possible (eqq. [A21], [A22]). Such plasticity in behavior would require parasites to act on cues such as the fraction of nests visited that contained a pale egg, in order to identify the best tactic. Hence, another fruitful line of empirical research would be to study the sampling of nests by potential conspecific parasites and, in particular, to explore whether or not and how their subsequent behavior is modified by the contents of sampled nests. In this context, it is important to note that the signal may not always be an egg that appears pale to human eyes. Identification of the aspects of egg appearance used as a signal would require careful investigation.

An implicit assumption of our model is that both the host and the parasite can benefit if the parasite is honestly

informed that the host has begun incubating its clutch. This will not always be so. If the parasite reacts to this information by destroying the clutch, perhaps in order to stimulate relaying, then the host clearly does not benefit from honestly informing the parasite that incubation has commenced. Cowbirds, which are interspecific brood parasites, have been known to destroy host clutches after the onset of incubation (Arcese et al. 1996). Hence, we would not expect such a signal to develop in conspecific parasitic systems in which clutch destruction is an effective strategy for the parasite. While clutch destruction to stimulate relaying may be an effective strategy for obligate interspecific brood parasites like cowbirds and cuckoos, it may be less effective for conspecific brood parasites that are likely to lay parasitic eggs over a shorter time interval and that have less control over the timing of individual egg production than obligate brood parasites. Hence, we suggest that this signaling system is more likely to arise in response to conspecific brood parasites.

There are alternative nonadaptive explanations for the last egg being a different color than the rest of the clutch. For example, it may be that physiological changes in the female as she completes egg laying and prepares to begin incubation may influence the function of pigment glands (Lowther 1988). Another explanation is that the pigment glands simply become depleted (Nice 1937). An alternative adaptive explanation is that pigment is expensive but provides a cryptic defence against predators. A bird can save on the expense of coloring the last egg, without increasing the risk from predation, because the eggs experience much higher parental attentiveness after the clutch is completed. The work presented here does not discount these mechanisms. Rather, it suggests that Yom-Tov's suggestion of an adaptive mechanism that would allow the evolution and maintenance of an odd-colored egg as a signal to potential brood parasites is plausible under certain circumstances. Hence, it would now seem appropriate to distinguish between these explanations. A first step toward this would be to use either natural variation or experimental manipulation to explore to what extent (if at all) brood parasites are dissuaded from laying in a nest by the presence of an odd-colored egg. Notice also that the existence of a nonadaptive reason for why final eggs should be pale (or otherwise different) does not prevent the use of that egg as a signal to brood parasites. Indeed, the methodology described above can be used to explore this situation if we assume that the final egg must be pale (nonsignaling, therefore, would not be an option for hosts) and that cheats produce another pale egg in addition to the final one. In fact, Lowther (1988) observed in house sparrow nests that, while in most nests only the last egg was pale, a very small fraction had an extra pale egg. Furthermore, Kendra et al. (1988) report that house sparrow

clutches contained only one pale egg and that this egg was not the final egg in the clutch. These observations are hard to reconcile with the other explanations given above but could be explained as cheats in the signaling mechanism. Now that we have demonstrated the theoretical plausibility of signaling, we hope that renewed effort will be invested into empirical testing of the necessary conditions for the development and maintenance of such a signal.

APPENDIX

Description of ESSs

We wish to find situations in which no individual would improve its net reward by unilaterally switching to a different strategy. To do this, we must calculate these net rewards for each strategy type. The net reward for a host playing the cheat strategy is

$$E[C] = V - E_1 - (1 - p)(1 - t)hC_1 - (1 - p)thC_2. \quad (\text{A1})$$

The first term is the value of the clutch, from which we subtract the cost of making the first egg pale, and the costs of being parasitized both before and after incubation begins.

The expected number of parasitic eggs laid before incubation starts is the number of parasites playing the non-receptive role (as these are the only parasites that will lay in a cheat's nest) divided by the number of available nests, $(1 - p)h$, multiplied by the probability that this is one of the nests that has not begun incubation when parasitic attack occurs $(1 - t)$. By similar reasoning, the expected number of parasitic eggs laid after incubation starts is $(1 - p)th$.

For honest signalers, the net reward is

$$E[H] = V - E_2 - (1 - p)(1 - t)hC_1 - (1 - p)thC_2 - \frac{p(1 - t)hC_1}{S}, \quad (\text{A2})$$

where S is the fraction of nests that do not contain a signal egg at the time when parasites attack:

$$S = s_3 + s_2(1 - t). \quad (\text{A3})$$

The last term requires some explanation. Honest signalers that have not completed their clutch and started incubation do not have a warning egg in their clutch and so are vulnerable to receptive parasites (as well as non-receptive ones). In this case, the number of available nests

for receptive parasites is not the total number of nests but only the total number of nests that contain no signal egg, hence the introduction of the S parameter in the last term.

The net reward to a nonsignaler is

$$E[N] = V - (1 - p)(1 - t)hC_1 - (1 - p)thC_2 - \frac{p(1 - t)hC_1}{S} - \frac{pthC_2}{S}. \quad (A4)$$

Nonsignalers pay no cost in producing a signal egg but are vulnerable to all parasites regardless of whether they have completed their clutch or not.

The net reward to nonreceptive parasites is easily calculated. It visits only one nest and receives a reward D if that nest does not have a complete clutch in it, which occurs with probability $(1 - t)$:

$$E[I] = (1 - t)D. \quad (A5)$$

The expected net reward to receptive parasites is more complicated. First, the parasite chooses a nest at random. If there is no signal egg in the nest, then the parasite lays an egg in that nest. It only gets a reward D from the egg if the clutch has not been completed, and hence the expected reward from the occasions when receptive parasites lay in the first nest they come to is $(s_2 + s_3)(1 - t)D$.

The probability that the first nest is rejected is simply $(1 - S)$. In this case, the parasite selects another nest at random; if it finds no signal egg in this nest, then it lays an egg in this nest, from which it gets a return of Dq , providing the host clutch has not been completed. Hence, the contribution to expected reward rate from occasions when the parasites lay in the second nest they consider is $(1 - S)(s_2 + s_3)(1 - t)Dq$. Summing up over all possible numbers of nest visited, we get

$$E[R] = (s_2 + s_3)(1 - t)D \left[1 + q(1 - S) + q^2(1 - S)^2 + q^3(1 - S)^3 + \dots \right] = \frac{(s_2 + s_3)(1 - t)D}{1 - q(1 - S)}. \quad (A6)$$

We can now use these expressions to look for the form of ESS solutions that are possible.

Case 1: Can All Three Host Strategies Coexist in an ESS Solution?

If this is the case, then we demand at the ESS that

$$E[C] = E[H] \Rightarrow E_1 - E_2 = \frac{p(1 - t)hC_1}{S} \quad (A7)$$

and that

$$E[H] = E[S] \Rightarrow E_2 = \frac{pthC_2}{S} \quad (A8)$$

so that

$$\frac{p}{S} = \frac{E_1 - E_2}{(1 - t)hC_1} = \frac{E_2}{htC_2}. \quad (A9)$$

Rearranging this, we get the condition

$$\frac{E_1}{E_2} = 1 + \frac{C_1(1 + t)}{C_2t}. \quad (A10)$$

Hence, we conclude that ESS solutions in which all three host strategies coexist occur only when parameter values are such that the condition above is satisfied. This is a nongeneric condition that we would not expect to occur, and so we will confine our search for ESS solutions to situations where fewer strategies occur.

Case 2: The Cheating and Nonsignaling Strategies Coexist and There Are No Honest Signalers (i.e., $s_2 = 0$)

It is easy to show that whenever $s_2 = 0$ and $s_1 > 0$, then $E[I] > E[R]$. Thus, we would expect all of the parasitic population to play the nonreceptive strategy so that $p = 0$:

$$p = 0 \Rightarrow E[N] - E[C] = E_1. \quad (A11)$$

Hence, nonsignalers always have a higher fitness than cheats, so no ESS exists with both cheats and nonsignaling individuals existing together.

Case 3: All Host Individuals Cheat ($s_2 = s_3 = 0$)

In this case, it is easy to show that nonreceptive parasites have a higher expected reward than receptive ones so, again, $p = 0$, and nonsignalers have a higher fitness than cheats. Hence, there is no ESS distribution in which all hosts cheat.

Case 4: All Host Individuals Are Honest ($s_1 = s_3 = 0$)

Under such circumstances,

$$E[R] = \frac{(1-t)D}{1-qt} > E[I]. \quad (\text{A12})$$

Thus, we would expect the whole parasite population to use the receptive strategy ($p = 1$). We require that, under such circumstances (i.e., $p = 1$, $s = 1 - t$), the honest strategy obtains a higher net reward than either of the other two:

$$E[H] > E[C] \Rightarrow E_1 > E_2 + hC_1, \quad (\text{A13})$$

$$E[H] > E[N] \Rightarrow E_2 < \frac{htC_2}{1-t}. \quad (\text{A14})$$

Thus, the situation in which all hosts are honest signalers and all parasites are receptive to that signal can be an ESS, but only if we satisfy the two conditions above.

Case 5: All Host Individuals Are Nonsignalers
($s_1 = s_2 = 0$)

When all hosts are nonsignalers, then both parasitic strategies produce identical rewards. We will consider the performance of invading honest and cheating signalers in the situation that is least favorable to nonsignalers, which occurs when all parasites are receptive (i.e., $p = 1$ and $S = 1$):

$$E[N] > E[H] \Rightarrow E_2 > thC_2, \quad (\text{A15})$$

$$E[N] > E[C] \Rightarrow E_1 > thC_1 + (1-t)hC_2. \quad (\text{A16})$$

Thus, if these two conditions are satisfied, then this is an ESS solution in which all hosts are nonsignalers, and both parasite strategies produce identical behavior and rewards.

Case 6: The Host Populations Contain Nonsignalers and Honest Signalers but No Cheats (i.e., $s_1 = 0$)

It is easy to show that when $s_1 = 0$ and $s_2 > 0$, then $E[R] > E[I]$, and so we would expect all parasites to be receptive to the signal (i.e., $p = 1$). We can also show that

$$E[H] - E[N] = \frac{htC_2}{1-s_2t} - E_2. \quad (\text{A17})$$

It is possible to solve this for the value of s_2 at which the payoffs to the two strategies are equal. Now consider what happens if we increase the number of honest signalers slightly above this, then $E[H] > E[N]$ (providing the value of p does not change), which would further encourage individuals to adopt honest signaling, moving the system further from equilibrium. We would not expect the value

of p to change from one, since more hosts switching to signaling would favor parasites that respond to that signal. Hence, although there is an equilibrium of this type, it is unstable and thus is not an ESS, and we would not expect it to have any biological significance.

Case 7: The Host Population Is a Mixture of Cheats and Honest Signalers, but There Are No Nonsignalers
(i.e., $s_3 = 0$)

When $s_3 = 0$, we find that

$$E[H] - E[C] = E_1 - E_2 - \frac{phC_1}{s_2}. \quad (\text{A18})$$

As in the last case, we see that when s_2 increases above the equilibrium value, $E[H] > E[C]$; providing p does not change with s_2 , the equilibrium is unstable. Hence, we must consider how p is affected by s_2 .

Case a. $E[R] < E[I]$, and thus $p = 0$. In this case, the relative fitness of honest and dishonest signalers is completely independent of s_2 and is not of interest to us, since the two strategies cannot coexist except in the trivial case where $E_1 = E_2$.

Case b. $E[R] > E[I]$, and thus $p = 1$. Increasing s_2 favors honest signalers, which in turn provides evolutionary pressure to increase s_2 further. Thus, once again, the equilibrium is not stable, and therefore it is not an ESS.

Case c. Assuming all strategies are strictly heritable, we can use the standard replicator dynamics (Hofbauer and Sigmund 1998) to consider how the population behaves when close to the equilibrium. Letting E_h be the mean fitness of the host population and E_p be the mean fitness of the parasite population, we obtain

$$\frac{dp}{dt} = p[E(R) - E_p] = p(1-p)[E(R) - E(I)], \quad (\text{A19})$$

$$\frac{ds_2}{dt} = s_2[E(H) - E_h] = s_2(1-s_2)[E(H) - E(C)]. \quad (\text{A20})$$

There is an equilibrium at $s = s_{2e}$ and $p = p_e$, where

$$s_{2e} = \frac{1-q}{1-q(1-t)},$$

$$p_e = \frac{(E_1 - E_2)(1-q)}{hC_1[1-q(1-t)]}. \quad (\text{A21})$$

It is easy to show that the equilibrium is unstable in this case.

Suppose now that parasite individuals can alter their tactics instantaneously. If $s_2 > s_{2e}$, then $E[R] > E[I]$. Thus, all individuals would play *R*, that is, $p = 1$. Thus, $E[H] < E[C]$, and so s_2 decreases to s_{2e} . If $s_2 < s_{2e}$, then $E[R] < E[I]$, that is, $p = 0$, and then $E[H] > E[C]$. Thus, s_{2e} would be the proportion of honest signalers in a mixture of honest signalers and cheats, and the parasite population would fluctuate maximally between everyone responding to the signal and everyone ignoring it. This would occur provided

$$E_1 - E_2 < \frac{hC_1[1 - q(1 - t)]}{1 - q}. \quad (\text{A22})$$

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