Should a Parasite Expose Itself?
(Some Theoretical Aspects of Begging and Vigilance Behavior)

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This paper examines the evolutionarily stable (ESS) solution of the begging conflict in cases involving nest parasitization. As expected, the presence in the nest of a parasite chick leads to a more intense begging conflict, with the parasite displaying a more selfish behavior than the host chicks. The model also predicts opposite responses by the host and the parasite to changes in the number of nestmates. While a larger number of nestmates entails a reduced ESS begging intensity for each of the host chicks, it entails an increased begging intensity for the parasite. Consequences of the parasite's ability to disguise itself are compared to analogous results for the vigilance game: whereas in the begging game a parasite should conceal itself, exposure can be selectively advantageous for a defector in the vigilance game.

There are many social interactions in nature in which the individual is faced with the familiar dilemma, either to "co-operate" or to "defect". By choosing to co-operate, the individual confers a common benefit on all group members, whereas defection yields a personal benefit only to the defector itself.

If the personal benefit caused by defection is greater than the personal benefit caused by co-operation, defection is the only evolutionarily stable strategy. But what happens if the benefit of co-operation is the greater? In such cases it is advantageous to co-operate, but even more advantageous to defect if other group members will nonetheless co-operate. Since this argument applies to all group members, so it seems again that natural selection will always favor the selfish strategy of defection.

The techniques of game theory have been used to show that in such situations an evolutionarily stable strategy (ESS, Maynard Smith & Price, 1973; Maynard Smith, 1982) that contains a certain amount of co-operation can exist. If this strategy is adopted by a population, no alternative rare ("mutant") strategy containing either a larger or a smaller degree of co-operation can invade and spread.

There are situations, however, in which asymmetries among group members can enable the establishment of a stable polymorphism, in which a small percentage of a less co-operative individuals coexists together with the common, more co-operative type. An interesting question then arises. Is it advantageous for the less co-operative type to expose itself, or should it conceal its parasitic nature? In an attempt to answer one such question, two different examples will be considered. The first, treated in some detail, examines the evolutionarily stable begging behavior among nestlings in nests which are also occupied by a chick of a nest parasite. Analogous results for the second example, the vigilance game, were obtained elsewhere (Motro & Cohen, 1989*a*) and will be presented here mainly for comparison.

Begging Among Nestlings

In many bird species, chicks in the nest solicit loudly and conspicuously for food, especially when a parent is present. This behavioral pattern, known as begging behavior, clearly indicates an intra-brood conflict, since by begging more loudly a chick can increase its share of the total amount of food provided by the parents to the nest. Unless there is some cost associated with begging, the intensity of begging will escalate and increase beyond all bounds (Dawkins, 1976; Stamps *et al.*, 1978; Macnair & Parker, 1979). But begging has its costs, namely, the extra expenditure of energy and the increased risk of predation. Whereas the first is a personal cost, borne by the solicitng chick itself, the risk of predation is a common cost, equally shared by all occupants of the nest.

Taking the cost of begging into account, game theory models (Macnair & Parker, 1979; Harper, 1986) have demonstrated that an ESS involving a finite and positive intensity of begging can exist. Moreover, a finite ESS exists even when there is no energy-associated personal cost, and the only cost is the higher risk of predation which is equally shared by all nestlings, regardless of their individual relative intensity of begging.

The presence in the nest of a genetically unrelated chick (a nest parasite, or "cuckoo") can alter the evolutionarily stable intensity of begging. To gain more insight into the possible consequences of this mutual interaction, I consider here a rather simple begging model, where the total amount of food available to a particular brood is fixed (Parker & Macnair, 1978; Macnair & Parker, 1978, 1979; Harper, 1986), and the cost of begging is equally shared by all individuals in the nest.

(1) FULL SIBS

Let $x \geq 0$ measure the intensity of soliciting of an individual, and let T be the sum of intensities of the entire brood. The parents dispense food in rations proportional to the relative begging intensity of each chick. Thus, a chick which begs with intensity x receives a proportion x/T of the total amount of food available to the nest.

Nest predators are attracted by the total intensity of begging of a nest. Hence the probability that a nest will be located by a predator is an increasing function of T, and the model assumes it has the form $1 - \exp(-T)$. Once a predator has located a nest, it will take all the chicks.

The fitness of an individual is assumed to be proportional to the product of its share of the food supply and the probability of surviving predation. Thus, the fitness of an individual having the begging strategy x is proportional to $(x/T) \exp(-T)$. (If $T = 0$, this expression is $1/n$, where n is the brood size.)

Clearly, if all the chicks were to co-operate (i.e. all have the same begging strategy $x = 0$) then each would obtain the same amount of food and the probability of predation will be minimal. But silence is not an ESS, and the evolutionarily stable solution of this conflict implies that all will eventually receive the same amount of food, but have a larger probability of predation.

To obtain the ESS consider a population fixed for a particular begging intensity x, and suppose a dominant mutation is introduced which causes its carriers to beg

with intensity x' ($x' \neq x$). If a mutant chick has k mutant sibs (and $n - k - 1$ sibs of the wild-type) its fitness is

$$W^{(k)}(x'; x) = \frac{x'}{(k+1)x' + (n-k-1)x} \exp\{-[(k+1)x' + (n-k-1)x]\}.$$

For a rare mutation, a mutant chick is usually a descendant of a mating between a wild-type and a heterozygous parent. Hence k has the binomial distribution with the parameters $n - 1$ and $0 \cdot 5$, and the (unconditional) fitness of the mutant is

$$W(x'; x) = \sum_{k=0}^{n-1} \binom{n-1}{k} \frac{1}{2^{n-1}} W^{(k)}(x'; x).$$

The ESS is obtained by solving the equation

$$\frac{d}{dx'} W(x'; x) \bigg|_{x'=x} = 0,$$

which implies

$$\sum_{k=0}^{n-1} \binom{n-1}{k} \frac{1}{2^{n-1}} [(n-k-1) - n(k+1)x] = 0,$$

which gives the ESS

$$x^* = \frac{n-1}{n(n+1)}.$$

The ESS is zero for broods of one chick, has a maximal value for $n = 2$ and $n = 3$, and tends to zero as brood size increases. This result is similar to that obtained by Harper (1986) for a slightly different model. The total begging intensity in an evolutionarily stable (ES) nest is

$$T^* = nx^* = (n-1)/(n+1),$$

which is a monotonically increasing function of n, and the fitness of an individual in an ES population is

$$W^* = (1/n) \exp[-(n-1)/(n+1)].$$

(2) THE PRESENCE OF A DETECTABLE NEST PARASITE

Harper (1986) concludes that nest parasites should beg more intensely than their nestmates of the host species. This section extends Harper's result.

Consider a nest with n ($n \geq 2$) chicks, $n - 1$ of which are full sibs and one is a genetically unrelated nest parasite. Let y be the begging strategy of the host species and z the begging strategy of the parasite.

The fitness of the parasite is

$$W_P(z; y) = \frac{z}{(n-1)y + z} \exp\{-[(n-1)y + z]\}.$$

By solving $dW_P(z; y)/dz = 0$, we get the parasite's best reply to y

$$\hat{z}(y) = -\tfrac{1}{2}(n-1)y + \tfrac{1}{2}\sqrt{[(n-1)y]^2 + 4(n-1)y}.$$

The fitness of a mutant host, having the strategy y' ($y' \neq y$), is

$$W_H(y'; y, z) = \sum_{k=0}^{n-2} \binom{n-2}{k} \frac{1}{2^{n-2}} W_H^{(k)}(y'; y, z),$$

where

$$W_H^{(k)}(y'; y, z) = \frac{y'}{(k+1)y' + (n-k-2)y + z} \exp\{-[(k+1)y' + (n-k-2)y + z]\}.$$

Solving $dW_H(y'; y, z)/dy'|_{y'=y} = 0$, we obtain

$$\sum_{k=0}^{n-2} \binom{n-2}{k} \frac{1}{2^{n-2}} \{[(n-k-2)y + z] - (k+1)y[(n-1)y + z]\} = 0,$$

which can be solved to yield the host's best reply to z,

$$\hat{y}(z) = \frac{1}{2(n-1)} \left\{ (n-2)/n - z + \sqrt{[(n-2)/n - z]^2 + 8(n-1)z/n} \right\}.$$

Note that $\hat{y}(z)$ is an increasing function of z. Thus the more selfishly the parasite behaves, the more selfish the host's best reply should be.

The ESS of this game with two types of players is given by the intersection of the best reply curves $\hat{z}(y)$ and $\hat{y}(z)$ (Motro, 1988). Thus we have

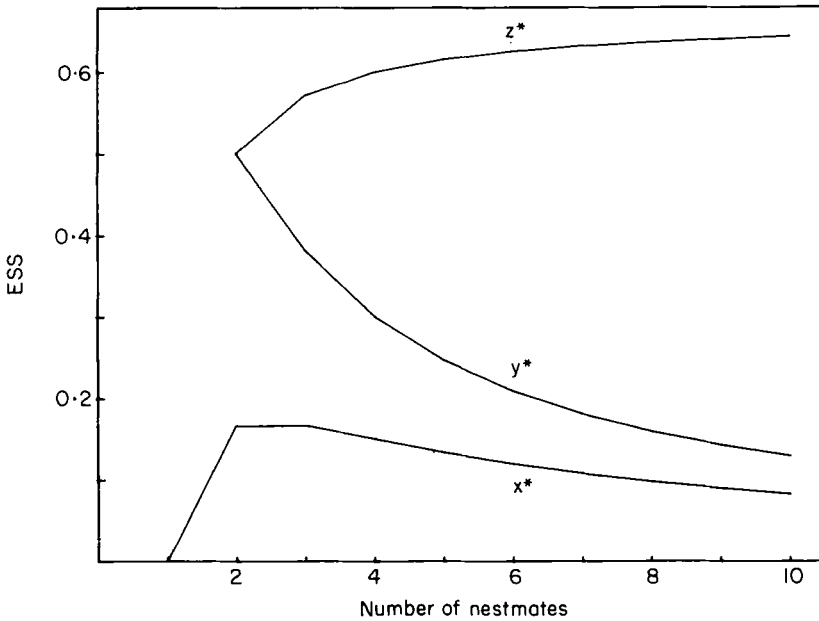$$y^* = \frac{4(n-1)}{n(3n-2)} \quad \text{and} \quad z^* = \frac{2(n-1)}{3n-2}.$$

FIG. 1. The evolutionarily stable begging intensities of the host and the parasite: x^* = The ESS with no parasitization, y^* = The ESS of the host in nests with a detectable nest parasite, z^* = The ESS of the detectable parasite.

From these explicit expressions we observe that the parasite's evolutionarily stable begging intensity (z^*) is larger than the host's ESS (y^*). (Except, of course, for $n = 2$, where both have the same value.) This outcome is in accordance with Harper's result. Moreover, we see that if the nest is parasitized, then the host's ESS (y^*) is always larger than the ESS of the preceding section (x^*), where nest parasites were not present. Thus in parasitized nests the host chicks increase their begging intensity, and the nest parasite begs even more loudly than they do. Although y^* is a *decreasing* function of n, the parasite's ESS (z^*) is an *increasing* function of n; a larger number of nestmates entails a reduced ESS begging intensity for each of the host chicks, but an increased begging intensity for the parasite.

The total begging intensity of a parasitized nest in an ES population is

$$T^* = (n-1)y^* + z^* = 2(n-1)/n,$$

and is a monotonically increasing function of n. The fitness of a host in an ES population is

$$W_H^* = \frac{2}{3n-2} \exp[-2(n-1)/n],$$

and the fitness of the parasite is

$$W_P^* = \frac{n}{3n-2} \exp[-2(n-1)/n].$$

(3) THE PRESENCE OF AN UNDETECTABLE NEST PARASITE

Suppose the nest parasite can disguise itself, so that it cannot be recognized as a parasite by the host chicks. In other words, the host cannot adjust its behavior according to the actual presence or absence of the parasite, but can only take into consideration the *possibility* of its presence. In this case the host's evolutionarily stable begging intensity has an intermediate value: the ESS is larger than x^* (the ESS in case there is no nest parasitization), but is smaller than y^* (the host's ESS in nests occupied by a detectable nest parasite). Here too the evolutionarily stable begging of the parasite is larger than the host's ESS, and is an increasing function of n, but it is smaller than z^* (the ESS in case the parasite can be detected) (see Appendix and Fig. 2).

Not surprisingly, the inability of the host to detect the presence of its parasite inflicts an additional load upon the host. Thus the host's fitness in an ES population (not shown) is smaller than the weighted average of its fitness in case the nest is not parasitized (case 1) and its fitness in case the nest contains a detectable nest parasite (case 2). The fitness of the undetectable parasite, however, is larger than the fitness of a detectable one (see Appendix). Thus by disguising itself, the nest parasite can increase its selective advantage. (Note that undetectability may have additional advantages for the parasite, such as avoiding being deprived of food by the host parent or preventing possible hostilities from the host chicks. These were
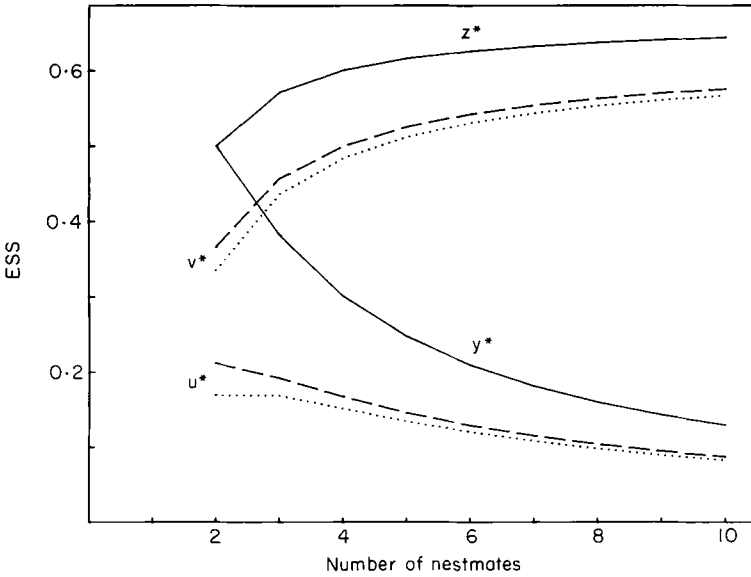
FIG. 2. The undetectable nest parasite: The evolutionarily stable begging intensities of the host (u^*) and the parasite (v^*) for a low frequency ($\pi = 0.01$, · · · · · ·) and a high frequency ($\pi = 0.20$, - - -) of parasitized nests. [The ESS of the host (y^*) and the parasite (z^*) in nests occupied by a detectable parasite (——) are given for comparison.]

not considered here. The only "weaponry" used in this model is the intensity of begging.)

The Vigilance Game

Vigilance for predators while feeding, also known as scanning behavior, presents a similar evolutionary problem, since a scanning individual gives up feeding. In choosing not to scan, the individual gains a personal benefit (through increased feeding), whereas scanning yields a benefit to all individuals in the group. Thus, for any individual it is clearly more beneficial that others will do the scanning, and that our individual will spend all its time feeding. Again, since such an argument applies to all other group members as well, it seems that natural selection will always favor the pure strategy of not scanning at all. However, game theory models (Pulliam *et al.*, 1982; Parker & Hammerstein, 1985; Motro & Cohen, 1989*a, b*; see also Hart & Lendrem, 1984; Lima, 1987, for different approaches) have demonstrated that under the plausible assumption of diminishing returns with regard to feeding efforts, a single evolutionarily stable vigilance strategy exists, which is represented by the probability of being vigilant at each time unit. (Using game theory terminology, the ESS is a mixed strategy, a mixture of the two pure strategies of "scanning" and "not-scanning".) Since it is assumed that even a single vigilant is sufficient to avoid

predators' success, it is not very surprising to find that in all the models, the evolutionarily stable vigilance probability decreases as group size (n) increases.

If the prevailing strategy in the population is the ESS, any mutant with a different vigilance strategy has a lower fitness, in particular a mutant adopting the pure selfish strategy of not scanning at all. However, as demonstrated by Motro & Cohen (1989a), if the other $n - 1$ group members can recognize the non-scanning defector, the above-mentioned ESS is no longer the best reply for the non-defectors, and another strategy, determining an increased level of vigilance, is then evolutionarily stable in the $n - 1$ player game (i.e. if adopted by the non-defectors, any one of them which changes its strategy decreases its own fitness). Moreover, adopting the new ESS increases the fitness of the non-defectors above their fitness had they all stuck to the former strategy. But more interesting is the fate of the recognizable defector: in the begging game, the host's best reply is an increasing function of the parasite's strategy, but in the vigilance game the best reply decreases as a function of the strategy of the defector. In other words, as a result of the defector's selfish behavior, the non-defectors, for their own self-interest, should be more co-operative. By forcing them to increase their co-operativeness, the recognizable defector can often increase its own fitness. Hence in such cases it may be advantageous for a defector to *advertize* its parasitic strategy, and for the other group members it may be best to *receive* that message and act accordingly. (The potential advantage to the recognizable defector is, indeed, frequency dependent, and an evolutionary process can be envisaged leading eventually to a stable polymorphism, in which both the recognizable social parasites and the co-operative individuals coexist together.)

Discussion

The begging conflict stems from the fact that by increasing its begging intensity, each chick can increase its own share of the food supply. However, intense begging decreases the survival probability of the entire brood, since it attracts predators. This conflict is moderated, to some extent, by kinship among the nestmates and possibly also by a direct personal cost to the soliciting chick (such as the loss of energy). Hence we can expect relatively selfish behavior (i.e. a higher intensity of begging) by a genetically unrelated nest parasite (Harper, 1986).

Further analysis of the mutual begging behavior in parasitized nests, carried out in this paper, shows as expected that the host's ESS is also altered: host chicks should beg more loudly, indeed, by a considerable amount. Less obvious, however, is the finding that while both the ESS of the host and the parasite depend on the number of nestmates, they show opposite responses to changes in the number of nestmates; whereas the host's ESS *decreases* as the number of nestmates *increases*, the parasite's evolutionarily stable begging intensity increases.

If the parasite cannot be detected, the host chicks can then react only to the possibility of its presence. For the host it results in an ESS having an intermediate value, intermediate between the ESS for the case of no parasitization and the host's ESS in nests occupied by a chick of a detectable parasite. For the parasite it also results in a lower ESS. Hence, if the parasite cannot be detected, the conflict in the

parasitized nest is thus subdued, and both the host and the parasite display lower intensities of begging. As for the fitness of the undetectable parasite, it turns out to be larger than the fitness of a detectable one. Thus, by disguising itself, a nest parasite can increase its selective advantage.

Then should a parasite always conceal its nature? The vigilance game shows that situations can exist in which a commited parasite benefits from exposing itself.

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APPENDIX

Let π be the frequency of the parasitized nests. If the parasite cannot be detected, the ESS of the host and of the parasite (u^* and v^*) are then functions of π. u^* and v^* have to satisfy

$$\frac{\mathrm{d}}{\mathrm{d}u'}\left[(1-\pi)W(u';u^*)+\pi W_H(u';u^*,v^*)\right]\Bigg|_{u'=u^*}=0 \qquad (A.1)$$

and

$$v^*=-\tfrac{1}{2}(n-1)u^*+\tfrac{1}{2}\sqrt{[(n-1)u^*]^2+4(n-1)u^*}. \qquad (A.2)$$

$dW(u'; u^*)/du'|_{u'=u^*}$ is zero for $u^* = x^*$, positive for $u^* < x^*$ and negative for $u^* > x^*$. Likewise, $dW_H(u'; u^*, v^*)/du'|_{u'=u^*}$ is zero for $u^* = y^*$, positive for $u^* < y^*$ and negative for $u^* > y^*$. Hence, for $0 < \pi < 1$, u^* satisfies $x^* < u^* < y^*$. ($u^* = x^*$ if $\pi = 0$, and $u^* = y^*$ if $\pi = 1$.)

The RHS of eqn (A.2) is an increasing function of u^*, having the value z^* for $u^* = y^*$. Hence $v^* < z^*$. Also, since $u^* < y^* \leq (n-1)/n$, we have $v^* > u^*$. Numerical solutions for u^* and v^*, over different values of π (some are shown in Fig. 2), confirm that v^* is an increasing function of n.

The fitness of the parasite in an ES population is

$$\frac{v^*}{(n-1)u^* + v^*} \exp\{-[(n-1)u^* + v^*]\} = (1 - v^*) \exp\{-[(n-1)u^* + v^*]\}$$

[where v^* is given by eqn (A.2)], and is a decreasing function of u^*. Since $u^* < y^*$, the fitness of the undetectable parasite is larger than that of a detectable one.