Helpers at Parents' Nest: A Game Theoretic Approach

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An overlapping-generations model is presented, which examines the evolution of helper-at-the-nest behavior. The basic conception in developing the model is that evolutionary stability, and not maximization of fitness (or inclusive fitness), should be considered as the criterion for evolution.

The model outlines the conditions for helping (or delayed dispersal), and the conditions for non-helping (early dispersal) to be evolutionarily stable, as well as the conditions under which both strategies are stable. The model also demonstrates the (quite anticipated) possibility for a parent–offspring conflict with respect to helping behavior.

Introduction

Helping-at-the-nest (or at-the-den), where non-breeding adults serve as auxiliaries and help the breeding pair in rearing the young (which are not direct descendants of the helpers), is a well-known phenomenon. Among the vertebrates, it has been documented in several hundred species of birds (for an illuminating compilation, see Skutch, 1987) and also in mammals and fish. The recent interest in this field is demonstrated by a number of books and reviews that appeared during the last decade (for example, Emlen & Vehrencamp, 1983; Emlen, 1984; Woolfenden & Fitzpatrick, 1984; Brown, 1987; Koenig & Mumme, 1987; Stacey & Koenig, 1990), as well as by many more specific articles.

In general, helpers are genetically related to the breeders they assist (and in most cases, direct descendants of the breeders, for example, Moehlman, 1979; Woolfenden & Fitzpatrick, 1984; Emlen & Wrege, 1988; Alves, 1990; Ligon & Ligon, 1990; Rabenold, 1990; Rowley & Russell, 1990; Walters, 1990). Therefore kin selection has been suggested as a probable mechanism for explaining the evolution of helping behavior in many cases. The basic assumption in all kin selection models of helping behavior (for example, Emlen, 1982; Brown & Pimm, 1985; Brown, 1987; Emlen & Wrege, 1989; Koford *et al.*, 1990) is that natural selection invariably operates to maximize inclusive fitness. However, in games between relatives this assumption is not necessarily correct, and the *stable* equilibria can be totally different from what is obtained by the maximization of the inclusive fitness (Eshel & Motro, 1981). Thus, the model presented in this paper explores the evolutionarily stable strategies (ESS, Maynard Smith & Price, 1973) of helping, and arrives to slightly different conclusions than those of the above-mentioned models.

Model I: Helping Decision is Made by the Helper

Consider a monogamous population of birds, where each individual has the same probability w of surviving to the next breeding season (or year). Thus, the life span of an individual has the geometric distribution, with mean $1/(1-w)$. Each juvenile has to choose one of two alternatives, either "help" or "disperse". Helpers remain with their parents for an additional breeding season, and help at the nest. Then, if still alive, they leave and breed on their own (see Emlen, 1982; Woolfenden & Fitzpatrick, 1984; Rowley & Russell, 1990). Non-helpers, on the other hand, leave and already breed at the next season, without spending any time as helpers. For simplicity, it is assumed here that helpers remain and help only if both parents are alive at that breeding season (and leave otherwise). The helping strategy of an individual is represented by a number $p(0 \leq p \leq 1)$, which is its probability of choosing to help. The assumption is that this strategy is genetically determined (by a single locus).

Assume broods of a constant size, n. A nest can either succeed (and produce n offspring) or fail (and produce none). The probability of success (π_L) is an increasing function of L, the number of helpers at that nest ($L = 0,1,\ldots,n$). If helpers' contributions are additive, then π_L is a linear function of L, that is, $\pi_L = \pi + Lb$, where π is the probability of success for a nest without helpers, and $b[b \leq (1-\pi)/n]$ is the contribution of each helper to the probability of success. Note that nb is the expected number of offspring contributed by each helper. Such additivity assumption (which is always valid for cases in which the brood consists of a single offspring) is not uncommon in previous models of helping-at-the-nest (for example, Brown & Pimm, 1985), and will be adopted also in this work. Additive effect of helpers is also suggested by several data sets, for example, in the white-fronted bee-eater (Emlen & Wrege, 1989), in the hoatzin (Strahl & Schmitz, 1990) and in the silver-backed jackal (Moehlman, 1979). However, Rabenold (1984) reports that in the stripe-backed wren, parental benefit depends on the number of helpers in a sigmoid way, whereas Woolfenden & Fitzpatrick's (1990) data illustrate a diminishing returns effect for the Florida scrub jay.

To obtain the evolutionarily stable helping strategies, consider a population that is fixed at a particular strategy p, and suppose a dominant mutation is introduced, which causes its carriers to choose to help their parents with probability x, $x \neq p$.

The payoff function considered in the overlapping-generations model presented here, is the expected number of *breeding* offspring of an individual that has already survived its first year. This payoff is equivalent to inclusive fitness, which incorporates both direct and indirect fitness components, but can more easily be calculated. Thus, the payoff of a mutant with a strategy x, introduced into a population which is fixed at p, will be denoted by $\Omega(x, p)$, and will be referred to simply as the fitness of the mutant.

Denote by ϕ_L the expected number of breeding offspring born to a mutant which has exactly L helpers. In particular, ϕ_0 is the expected number of breeding offspring born to a mutant which does not have any helpers.

If both parents of a young mutant are still alive at the next breeding season (the probability of this event is w^2), the mutant then can either help (with probability x)

or leave (with probability $1-x$). In the former case, it leaves only towards the following breeding season, if still alive. In any case, since helpers only help if both parents are together, an individual cannot have any helpers on its first breeding attempt. Hence,

$$\Omega(x, p) = w^2[(1-x)\phi_0 + xw\phi_0] + (1-w^2)\phi_0 = \phi_0[1 - w^2(1-w)x]. \tag{1}$$

ϕ_0 is calculated as follows: The brood of a breeding mutant, which has exactly L helpers, can either succeed (with probability π_L) or fail (with probability $1-\pi_L$). In the latter case, ϕ_L simply equals $w\phi_0$. If the brood succeeds, then ϕ_L equals n, if the mutant dies before the next breeding season, and ϕ_L equals $n+\phi_0$, if its mate, but not the mutant, dies before the next breeding season. (Recall that helpers only help if both parents are alive, hence in the next breeding season the mutant will have to breed without any help.) If both parents survive, then if on the next breeding season they are helped by, say, M helpers, ϕ_L is equal, under this condition, to $n - M + wM + \phi_M$. Since the number of helpers M has the binomial distribution with the parameters n and $\frac{1}{2}(x+p)$, the unconditional value of ϕ_L equals $n - \frac{1}{2}(1-w)(x+p)n + \bar{\phi}$ (where $\bar{\phi}$ is the expected value of ϕ_M with respect to M). To conclude,

$$\phi_L = (1-\pi_L)w\phi_0 + \pi_L\{(1-w)n + w(1-w)(n+\phi_0) + w^2[n - \tfrac{1}{2}(1-w)(x+p)n + \bar{\phi}]\}$$

$$= w\phi_0 + \pi_L\{[1 - \tfrac{1}{2}w^2(1-w)(x+p)]n + w^2(\bar{\phi} + \phi_0)\}, \tag{2}$$

where $\pi_L = \pi + Lb$. In particular,

$$\phi_0 = w\phi_0 + \pi\{[1 - \tfrac{1}{2}w^2(1-w)(x+p)]n + w^2(\bar{\phi} - \phi_0)\}. \tag{3}$$

Taking expectation (with respect to L) in eqn (2), we get

$$\bar{\phi} = w\phi_0 + [\pi + \tfrac{1}{2}(x+p)nb]\{[1 - \tfrac{1}{2}w^2(1-w)(x+p)]n + w^2(\bar{\phi} - \phi_0)\}. \tag{4}$$

Equations (3) and (4) then yield

$$\phi_0 = \frac{\pi[1 - \tfrac{1}{2}w^2(1-w)(x+p)]n}{(1-w)[1 - \tfrac{1}{2}w^2(x+p)nb]}. \tag{5}$$

Inserting ϕ_0 into eqn (1), we obtain the fitness of the mutant

$$\Omega(x, p) = \frac{\pi[1 - \tfrac{1}{2}w^2(1-w)(x+p)][1 - w^2(1-w)x]n}{(1-w)[1 - \tfrac{1}{2}w^2(x+p)nb]}. \tag{6}$$

$\Omega(x, p)$ has a maximum with respect to x at either $x=0$ or $x=1$. Thus, if $\Omega(0, p) > \Omega(1, p)$, the mutant's best-reply is $x=0$, and if $\Omega(0, p) < \Omega(1, p)$, the mutant's best-reply is $x=1$. Denote

$$A_1(w) = \frac{(1-w)[3 - 2w^2(1-w)]}{1 + w^2(1-w) - [w^2(1-w)]^2}$$

$$A_2(w) = (1-w)[3 - w^2(1-w)].$$

For $0 < w < 1$, $A_1(w) < A_2(w)$, and both are decreasing functions of w.

It turns out that if $nb < A_1(w)$, the mutant's best-reply is $x = 0$ for all p, thus the ESS is $p^* = 0$.

If $nb > A_2(w)$, the mutant's best-reply is $x = 1$ for all p, thus the ESS is $p^* = 1$.

However, if $A_1(w) < nb < A_2(w)$, a value $\tilde{p}$ $(0 < \tilde{p} < 1)$ exists, such that if $p < \tilde{p}$, the mutant's best-reply is $x = 0$, whereas if $p > \tilde{p}$, the best-reply is $x = 1$. Thus, in this case, two ESSs exist, namely, $p^* = 0$ and $p^* = 1$.
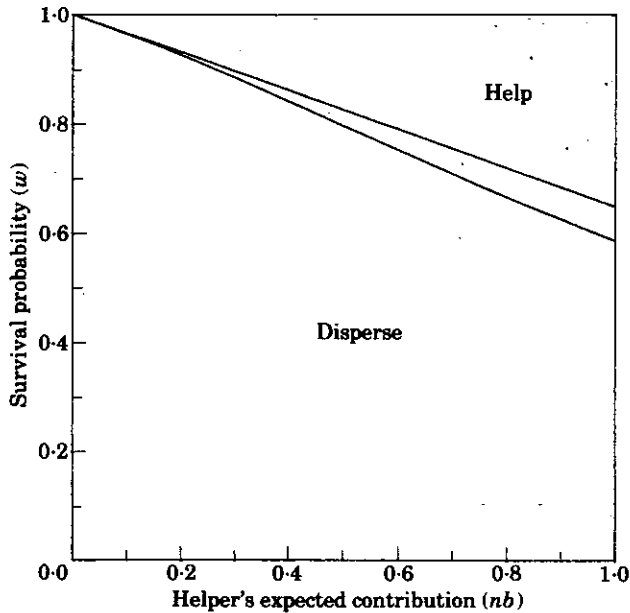

FIG. 1. The ESS of helping under offspring control. (In the intermediate zone of the parameter space, both "help" and "disperse" are evolutionarily stable.)

To summarize (see Fig. 1), if the expected contribution of a helper (nb) is small, then dispersal is the only ESS; if the helper's expected contribution is large, then helping is the only ESS; whereas both these pure strategies are evolutionarily stable if the expected contribution has an intermediate value (as defined above).

Likewise, from the viewpoint of survival probability, if the probability of an individual to survive to the next breeding season (w) is small, then dispersal is the only ESS; if the survival probability is large, then helping is the only ESS; while both strategies are evolutionarily stable if the survival probability has an intermediate value.

Current models of helping-at-the-nest, which consider maximization of inclusive fitness, generally present a single inequality, such that either helping *or* dispersal is advantageous (thus, it is implied, should be maintained by the population), according to whether or not this inequality is fulfilled. However, the ESS model presented here shows that natural selection operates in a more complex way, and that situations can exist, for example, where both pure strategies are evolutionarily stable.

Model II: Helping is Imposed by the Parent

Suppose that the decision whether to stay and help or to disperse and breed is not made by the offspring itself, but by its parent (the father, say), according to the parent's own genotype. Thus, if the population is fixed at a helping strategy p, the probability of a mutant with a helping strategy $x \neq p$ to become a helper is either x (if it inherited the mutation from its father) or p (if it inherited the mutation from its mother). Hence, the fitness of the mutant is

$$\Omega(x, p) = w^2\{[1 - \tfrac{1}{2}(x+p)]\phi_0 + \tfrac{1}{2}(x+p)w\phi_0\} + (1-w^2)\phi_0$$
$$= \phi_0[1 - \tfrac{1}{2}w^2(1-w)(x+p)]. \tag{7}$$

If the mutant is a male, his expected number of helpers as a breeder is nx, whereas if the mutant is a female, her expected number of helpers is np. In the former case,

$$\phi_0 = \frac{\pi[1 - w^2(1-w)x]n}{(1-w)(1 - w^2xnb)}, \tag{8}$$

and in the latter case,

$$\phi_0 = \frac{\pi[1 - w^2(1-w)p]n}{(1-w)(1 - w^2pnb)}. \tag{9}$$

If the mutant has the same probability of being either a male or a female, the fitness is

$$\Omega(x, p) = \frac{\pi n}{2(1-w)}\left[\frac{1 - w^2(1-w)x}{1 - w^2xnb} + \frac{1 - w^2(1-w)p}{1 - w^2pnb}\right][1 - \tfrac{1}{2}w^2(1-w)(x+p)]. \tag{10}$$

$\Omega(x, p)$ has a maximum with respect to x at either $x=0$ or $x=1$. Thus, if $\Omega(0, p) > \Omega(1, p)$, the mutant's best-reply is $x=0$, and if $\Omega(0, p) < \Omega(1, p)$, the mutant's best-reply is $x=1$. Denote

$$B_1(w) = \frac{(1-w)[2 - \tfrac{1}{2}w^2(1-w)]}{1 + \tfrac{1}{2}w^2(1-w)}$$

$$B_2(w) = \frac{\tfrac{1}{2}(1-w)[4 - 3w^2(1-w)]}{1 - \tfrac{1}{2}w^2(1-w)}.$$

For $0 < w < 1$, $B_1(w) < B_2(w)$, and both are decreasing functions of w.

It turns out that if $nb < B_1(w)$, the mutant's best-reply is $x=0$ for all p, thus the ESS is $p^* = 0$.

If $nb > B_2(w)$, the mutant's best-reply is $x = 1$ for all p, thus the ESS is $p^* = 1$.

However, if $B_1(w) < nb < B_2(w)$, a value $\tilde{p}(0) < \tilde{p} < 1$ exists, such that if $p < \tilde{p}$, the mutant's best-reply is $x = 1$, whereas if $p > \tilde{p}$, the best-reply is $x = 0$. At $\tilde{p}$, $\Omega(0, \tilde{p}) = \Omega(1, \tilde{p})$. Since the fitness $\Omega(x, \tilde{p})$ of a mutant with any mixed strategy $0 < x < 1$ (and with $\tilde{p}$ in particular), is smaller than $\Omega(0, \tilde{p})$ and $\Omega(1, \tilde{p})$, $\tilde{p}$ is not an ESS. [In fact, the assumption in Bishop & Cannings' (1978) theorem is that the payoff to a mixed
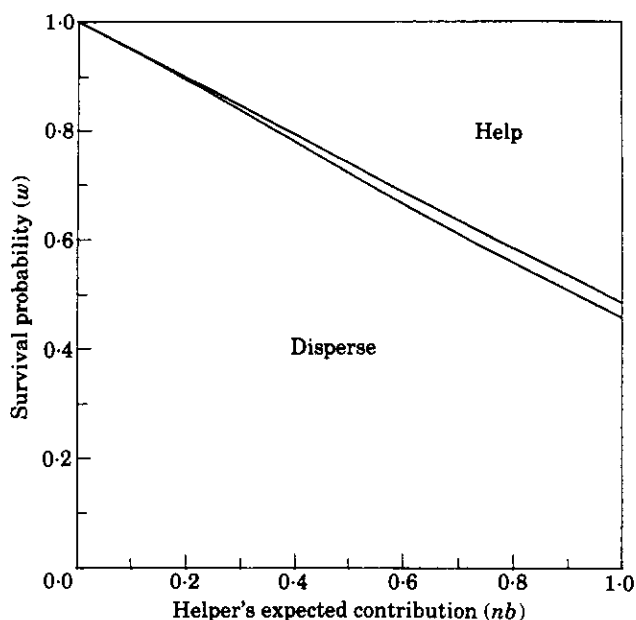
FIG. 2. The ESS of helping under parental control. (In the intermediate zone of the parameter space, no ESS exists.)

strategy is always the average of the payoffs to the corresponding pure strategies. This, however, is not the case in our model.] Thus, if $B_1(w) < nb < B_2(w)$, there is no ESS.

To summarize (see Fig. 2), if the expected contribution of a helper (nb) is small, the ESS is to disperse the progeny; if the helper's expected contribution is large, the ESS is to retain the offspring as helpers; whereas if the expected contribution has an intermediate value (as defined above), no ESS exists.

Likewise, from the viewpoint of survival probability, if the probability of an individual to survive to the next breeding season (w) is small, the ESS is to disperse the progeny; if the survival probability is large, the ESS is to impose helping; and no ESS exists if the survival probability has an intermediate value.

Note that $B_2(w)$ is smaller than $A_1(w)$ (for $0 \leq w < 1$). Thus, over part of the parameter space, the parental ESS is that of retaining the offspring as helpers, while the offspring ESS is to leave and breed (compare Figs 1 and 2). This demonstration of the possibility for a parent–offspring conflict is not surprising (see also Emlen, 1982), although Brown & Pimm (1985) predicted that there should be no parent–offspring conflict under the overlapping generation model. In a recent paper, Emlen & Wrege (1992) report that "older male white-fronted bee-eaters (typically fathers) actively disrupt the breeding attempts of their sons, and that such harassment frequently leads to the sons joining as helpers at the nest of the harassing father".

The "optimal" strategy of helping, that which produces the *maximal* payoff, is the same strategy under either parental or offspring control (hence the result of Brown

& Pimm, 1985). It is obtained by setting $x = p$ in either eqn (6) or eqn (10), and then finding the value of p that maximizes the fitness. Thus, dispersal is optimal if $nb < (1-w)[2-w^2(1-w)]$, whereas helping is optimal if $nb > (1-w)[2-w^2(1-w)]$. Note that $B_2(w) < (1-w)[2-w^2(1-w)] < A_1(w)$. Hence the fitness-maximizing strategy lies between the two ESSs, that of the offspring and that of the parent, and prescribes a helping behavior which is more altruistic than that implied by the ESS of the offspring, yet more selfish than that implied by the ESS of the parent. However, the optimal strategy is not evolutionarily stable, and cannot be maintained under natural selection.

Discussion

If helpers are genetically related to the breeders they assist (hence also to the young they help to raise), kin selection is sufficient to explain the evolution of helper-at-the-nest systems, as has been demonstrated by several theoretical models, including the overlapping-generations model presented in this work. This does not preclude other factors, such as self-interest, personal advantage (Zahavi, 1974) or ecological and demographic constraints, from enhancing the evolution of helping behavior, in particular in cases involving help among non-kin.

The essential difference between the model developed here and the previous models of helpers-at-the-nest is in considering evolutionary stability, and not inclusive fitness maximization, as the appropriate criterion for evolution. This more correct approach produces results that are generally in accordance with those of the other models. Nevertheless, it demonstrates the possibility of a parent–offspring conflict with respect to helping behavior (compare with Brown & Pimm, 1985; but see Emlen, 1982; Emlen & Wrege, 1992). The model also points out to the possibility that in certain cases, both pure strategies of helping, namely "help" and "disperse", can simultaneously be stable. In such cases, the population can be fixed at either strategy, depending on initial conditions.

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