DELAYED DISPERSAL AND REPRODUCTION AS A LIFE-HISTORY TACTIC IN COOPERATIVE BREEDERS: FITNESS CALCULATIONS FROM RED-COCKADED WOODPECKERS

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Abstract.—The evolution of delayed dispersal and reproduction in cooperative breeders can be viewed as selection between alternative life-history tactics: (1) stay-and-foray (SAF), in which individuals delay dispersal and reproduction and compete for breeding vacancies in the vicinity of the natal territory, and (2) depart-and-search (DAS), in which individuals disperse soon after fledging to wander in search of a breeding vacancy. Using demographic data collected from red-cockaded woodpeckers (Picoides borealis), we evaluated a demographic model of the evolution of delayed dispersal and reproduction based on selection between these tactics. Because males of this species exhibit both tactics regularly, we could estimate all model parameters directly. Our estimates provide empirical support for key assumptions of demographic models of the evolution of delayed dispersal and reproduction, such as a disparity in survival between those adopting SAF and those adopting DAS during the first year of life, a low rate of successful dispersal in those practicing DAS, and low reproductive success at early ages among breeders. We show, in a population in which the fate of dispersers could be documented, that the fitness of individuals delaying dispersal and reproduction can equal or exceed that of individuals attempting early reproduction, even without indirect fitness benefits due to helping behavior.

Cooperative breeding refers to a social system in which some individuals (helpers) assist in rearing young produced by other conspecifics (Brown 1978, 1987; Emlen and Vehrencamp 1983; Emlen, in press). In most species of cooperative breeders, helpers are nonbreeders that remain on their natal territory and assist one or both parents. Delayed reproduction and delayed dispersal in such species may be viewed as life-history tactics, and the evolution of such behavior as selection between alternative life-history tactics (Emlen 1982a; Wooffenden and Fitzpatrick 1984; Brown 1985, 1987). The tactic of those that delay dispersal and reproduction is to remain on the natal territory and wait for a breeding vacancy in the vicinity that they can fill, either on the natal territory itself or on a nearby territory, that is, stay-and-foray (SAF; Brown 1987, p. 103). The alternative is to disperse after fledging in search of a territory. This depart-and-search tactic (DAS; Brown 1987, p. 103) is employed by most noncooperative birds and is the more common tactic. Retention of young thus arises because of selection for SAF over DAS under particular conditions. Why retained young engage in helping
behaviors such as feeding nestlings is a separate evolutionary question (Brown 1974, 1987; Emlen 1982a, 1982b).

The dichotomy in dispersal behavior that characterizes the tactics is not just a theoretical construct. The dichotomy has been observed in several species (Rowley 1965, 1981; Austad and Rabenold 1986; Woolfenden and Fitzpatrick 1986; Walters et al. 1988).

Why might SAF be selected? One advantage of SAF is that its practitioners have an advantage in competing for breeding vacancies in the vicinity of their territory (Lewis 1982; Zack and Rabenold 1989; Emlen, in press). Thus SAF may be an effective strategy in competing for limited and valuable resources, whether they be high-quality territories (Stacey and Ligon 1987; Powell 1989) or breeding vacancies in large groups (Wiley and Rabenold 1984; Zack and Rabenold 1989). Many cooperative breeders are characterized by an apparent shortage of suitable territories, a condition that has been termed habitat saturation (Selander 1964; Brown 1969; Stacey 1979). This presumably reduces the probability of successful dispersal and thus the payoff of DAS. Poor reproductive capacity of young birds also reduces the payoff of DAS (Brown 1987, p. 65).

Advantages of group living also may contribute to the payoff of SAF. Those adopting SAF live in familiar surroundings, in the company of others who may assist them in locating food or detecting predators, and may enjoy indirect as well as direct fitness benefits if their assistance increases the reproductive success of their group. Reproductive success increases with group size in some cooperative breeders (Brown et al. 1982; Rabenold 1984; Austad and Rabenold 1985; Reyer and Westerterp 1985), although in many no effect independent of territory quality is evident (Koenig and Mumme 1987, chap. 6).

The demographic conditions under which delayed dispersal and reproduction can evolve through selection of SAF over DAS have been modeled by many (Vehrencamp 1979; Emlen 1982a; Stacey 1982; Wiley and Rabenold 1984; Woolfenden and Fitzpatrick 1984; Brown 1985, 1987). These models represent an accounting of fitness, measured in terms of lifetime reproductive success, using survival and reproductive schedules under the alternative life-history tactics. Advantages of group living, low probabilities of dispersal, low fecundity at young ages, and other factors all can be incorporated into this accounting. This approach, although widely accepted, lacks empirical support. The difficulty of determining the fate of dispersers has been a particularly insidious problem. The purpose of this study is to provide empirical evidence, from a population in which the fate of dispersers could be documented, that these models accurately describe the demographic conditions that exist in a cooperatively breeding species. We calculate expected lifetime reproductive success and two other measures of fitness for both tactics, using data collected from a population study of the red-cockaded woodpecker (Picoides borealis), and show that average fitness is roughly equal for the two tactics in a population in which both are commonly employed. We show that the fitness of individuals that delay dispersal and reproduction can equal or exceed that of individuals that attempt to reproduce early, even without indirect fitness benefits of helping behavior.
THE STUDY SPECIES

The red-cockaded woodpecker is an endangered cooperative breeder endemic to the pine savannas of the southeastern United States (Thompson 1971; Wood 1983; U.S. Fish and Wildlife Service 1985; Ligon et al. 1986; Walters 1990). Groups consist of a pair of breeders and 0–4 nonbreeding male helpers (Lennartz et al. 1987; Walters et al. 1988; Walters 1990). Many social units lack helpers, and few include more than one helper. Female helpers are rare. The majority of helpers reside on their natal territory and assist both parents or their father and an unrelated female. Helpers apparently do not copulate, regardless of their relatedness to the breeding female (Lennartz et al. 1987; Lape 1990), so direct reproduction by helpers may be ignored. Only one brood is raised per year, which simplifies measurement of annual reproductive success.

Red-cockaded woodpeckers are well suited for making the fitness calculations described above because both DAS and SAF occur at a relatively high frequency. Operationally, males adopting the two tactics can be distinguished according to their location at age 1 yr (see below). Many males (69% of males surviving to age 1 in our study population) remain on their natal territories as helpers at age 1 (SAF males). These males become breeders by inheriting breeding status on the natal territory or by dispersing to a nearby territory (65% to a contiguous territory). Other males (31% of males surviving to age 1) disperse in their first year (DAS males). Some (39%) of these are breeders on other territories at age 1. That these males disperse farther (median = 4.5 km) than fledgling females (median = 3.2 km) on average, that their median dispersal distance is farther than the maximum dispersal distance recorded for a helper (4.0 km), and that many (56%) end up as solitary males (territory but no mate) or floaters (neither territory nor mate) indicate that these males, like most females, adopt DAS (Walters et al. 1988).

The payoffs of the two tactics therefore can be measured directly in red-cockaded woodpeckers. In most other species of birds, the payoff of only one tactic is easily measured and the payoff of the other must be estimated indirectly (see, e.g., Woolfenden and Fitzpatrick 1984), an approach that necessitates making many assumptions. In noncooperative species SAF is absent, whereas in cooperative species DAS may be rare, or its payoff simply is difficult to measure.

THE MODEL

The model used to estimate fitness is derived from that of Woolfenden and Fitzpatrick (1984). The payoff of the DAS tactic in their model may be expressed as

$$L_d TR,$$

where $L_d$ is the probability of a dispersing bird’s surviving to the end of age interval 0 (fledging to age 1 yr), $T$ is the probability that a surviving disperser will acquire breeding status at age 1, and $R$ is the lifetime reproductive success of
breeders, which is assumed to be independent of the age at which breeding begins. In the Woolfenden and Fitzpatrick (1984) model, birds adopting DAS either become breeders at age 1 or perish. The payoff of the SAF tactic may be expressed as

$$L_hk + L_hRB \sum_{i=2}^{n} (L_{1i})^{(i-1)} (1 - B)^{(i-2)},$$  \hspace{1cm} (2)$$

where $L_h$ is the survival of birds remaining on the natal territory to age 1 yr; $k$ is the increment in indirect reproduction for a helper due to that helper’s assistance, that is, the increase in group reproductive success attributable to the helper, devalued by the relatedness of the helper to the young (see eq. [7] below); $B$ is the annual probability that a breeding vacancy will arise that the helper can fill (assumed constant with age); $L_{1i}$ is the annual survival rate of helpers after the first year; $i$ is the age at which a helper becomes a breeder; and $n$ is maximum age. Helpers remain on the natal territory until becoming breeders at age $i$. The fraction surviving to age 1 is $L_{1i}$, and they produce $k$ offspring indirectly through helping relatives at age 1. They are credited with no additional indirect fitness component for helping at ages 2 through $i$ and produce $R$ offspring regardless of the age at which breeding begins.

To apply this model to red-cockaded woodpeckers, we relaxed some of the simplifying assumptions of Woolfenden and Fitzpatrick (1984). Specifically, we allowed helpers to accrue indirect fitness benefits beyond age 1, and we used age-specific reproductive parameters rather than assume that $R$ was independent of age. We further increased the complexity of the model to reflect observed peculiarities of the social system of the woodpeckers. We allowed those adopting DAS to become solitary males or floaters, as well as breeders, at age 1. Although such males did not reproduce at age 1, they had a nonzero probability of becoming breeders in subsequent years. We modeled this in the same way as acquisition of breeding status by helpers. The payoff of the DAS tactic is expressed as follows:

$$L_dT \sum_{x=1}^{n} p_b^{(x-1)} m_x + L_dFp_fG \sum_{x=2}^{n} p_b^{(x-2)} m_x$$

$$+ \sum_{i=2}^{n} L_d(1 - T - F)p_s^{(i-1)}S(1 - S)^{(i-2)} \sum_{x=i}^{n} p_b^{(x-2)} m_x,$$  \hspace{1cm} (3)$$

where $p_b$ is the annual probability of survival of breeders; $m_x$ is fecundity at age $x$, measured in gene-equivalents (identical to male offspring 50% related to self, assuming an even sex ratio); $F$ is the probability that a surviving disperser will be a floater at age 1; $p_f$ is the annual probability of survival of floaters; $G$ is the annual probability that a floater will become a breeder; $S$ is the annual probability that a solitary male will become a breeder; and $p_s$ is the annual probability of
survival of solitary males. The payoff of the SAF tactic is expressed as follows:

\[ L_h k + L_h \sum_{i=2}^{n} p_h^{(i-1)} (1 - B)^{(i-2)} \left[ k(1 - B) + B \sum_{x=i}^{n} p_b^{(x-2)} m_x \right] , \]  

(4)

where \( p_h \) is the annual probability of survival of helpers. Sums are from 1 to \( n \) or 2 to \( n \) rather than 0 to \( n \) so that \( x \) is equivalent to age. We allow floaters to become breeders at age 2 but assume that no floaters that fail to become breeders at age 2 survive to age 3. We allow birds to remain in the solitary male class indefinitely. Thus, those adopting DAS may become breeders at age 1 (eq. [3], first term), floaters at age 1 and breeders at age 2 (second term), or solitary males at age 1 and breeders at age \( i \) (third term).

We assume that mortality of breeders, helpers, and solitary males is independent of age and that the probabilities of helpers' and solitary males' becoming breeders are independent of age. Our data indicate no dependence on age for any of these parameters except mortality of breeders. Mortality of breeders appears to be higher at age 1, and lower at ages 2–4, than at older ages. However, including age-specific breeder mortality had no effect on the results. Therefore, the simplifying assumption of age-independent breeder mortality was retained.

Equations (3) and (4) cannot be compared directly because of the problem of double accounting (Grafen 1982; Brown 1987, p. 57); that is, extra offspring resulting from helping are credited to both the helper and the breeder in the equations. We therefore separated direct and indirect reproduction in equation (4) as follows:

\[ L_h \sum_{i=2}^{n} p_h^{(i-1)} (1 - B)^{(i-2)} B \sum_{x=i}^{n} p_b^{(x-2)} m_x , \]  

(5)

direct,

and

\[ L_h k + L_h \sum_{i=2}^{n} p_h^{(i-1)} (1 - B)^{(i-1)} k . \]  

(6)

indirect,

Equations (3) and (5) may be compared to determine whether SAF is favored even in the absence of helping behavior (i.e., assisting breeders in reproduction; Brown 1987, p. 235). The effect of helping behavior on relative payoffs can then be assessed from equation (6). Future components of indirect fitness (Brown 1987, p. 55; Mumme et al. 1989) are unlikely in this species and therefore are not included in fitness calculations.

The apparent effects of helpers on reproductive success in our study population likely are partly or wholly an artifact of territory quality (Manor 1991). When we compared the reproductive success of the same pair of breeders on the same territory with and without helpers in consecutive years, we found only a small
effect of helpers. Therefore we focus on the direct component of fitness, that is, on comparisons involving equations (3) and (5).

METHODS

We collected the data used to test the model from a population of red-cockaded woodpeckers in the Sandhills region of south-central North Carolina from 1980 to 1987. The habitat in the 110,000-ha study area generally is second-growth longleaf pine (Pinus palustris) with scattered old-growth trees, an understory of oaks (Quercus spp.), and ground cover of wire grass (Aristida stricta). The study area is described in detail in Carter et al. (1983) and Walters et al. (1988).

Resident adults were banded at the beginning of the study with unique combinations of colored leg bands. Each year all nestlings and unbanded adult immigrants were banded similarly. Adults were sexed using the presence (males) or absence (females) of the red cockade, a small patch of red feathers just behind the eye at the margin of the bird’s white cheek patch. Young were sexed as fledglings using the presence (males) or absence (females) of a red crown patch. Roughly 225 groups of red-cockaded woodpeckers resided in the study area (218–234, depending on year), and each group was censused every breeding season. The members of the group were identified, and the status of each (breeding male, helper male, floater female, etc.) was determined. Reproduction of each group was monitored, culminating in identification of young fledged. Details of methods related to censusing and monitoring reproduction are given in Walters et al. (1988).

Estimation of Model Parameters

We measured survival and transition probabilities from one breeding census to the next. For example, we estimated survival of breeders as the proportion of breeders present in one breeding census still alive in the next breeding census and the probability that a breeding vacancy arises that a helper fills as the proportion of helpers present in one breeding census and still alive the next that have become breeders in the second breeding census. We computed age-specific fecundity as the average number of fledglings produced by breeders of that age. We could compute values for each age through age 5 but had to combine data to produce a single estimate for birds age 6 and older because of small sample sizes. We set maximum age at 13 yr. The oldest birds of unknown age in the population were at least 10 yr old, and 9% of the members of our oldest known-age cohort were still living at age 8.

We computed \( k \) in terms of gene-equivalents, with relatedness to helper of 100%, so that direct and indirect fitnesses were measured in the same currency. We estimated \( k \) as

\[
(1 - H)t(M_h - M_0),
\]

where \( H \) is the fraction of helpers that are the second, third, or fourth helpers in their group; \( t \) is the average relatedness between helpers and the young they help.
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raise; \(M_h\) is the number of young fledged by groups with helpers; and \(M_0\) is the number of young fledged by groups without helpers. The first term is necessary so that the total increment in reproductive success is not credited to each helper in groups with multiple helpers.

Two parameters, \(L_d\) and \(L_h\), are particularly difficult to estimate. Determining which tactic is adopted by fledglings that survive their first year is straightforward. Those remaining on their natal territory at age 1 we assumed to be following SAF, whereas those that had dispersed to another territory by age 1 we assumed to be following DAS. Males make an apparently unambiguous choice between SAF and DAS during their first year. We have never observed a male practicing DAS to return to its territory after departing it, and we rarely have observed helpers to disperse long distances, that is, to switch from SAF to DAS. Thus, surviving birds can be assigned to one tactic or the other. Estimation of the overall survival of fledglings to age 1 also is straightforward. What is difficult to determine is to which tactic those that perish should be assigned. We did this in three ways.

1. We used the female survival rate in the first year as an estimate of \(L_d\), because females follow DAS. Thus \(L_d\) and the numbers of survivors employing SAF, \(X_h\), and DAS, \(X_d\), are known. Let \(N_h\) and \(N_d\) equal the number of fledglings adopting DAS and SAF, respectively, and let \(N = N_h + N_d\). Then \(L_h\) can be computed as follows:

\[
N_d = X_d / L_d; \tag{8}
\]

\[
L_h = X_h / (N - N_d). \tag{9}
\]

2. We censused a sample of 124 groups during the winter of 1984–1985 and 134 groups during the winter of 1985–1986. This enabled us to identify a number of first-year males adopting DAS on the basis of their having dispersed from their natal territory by winter. We could then calculate the survival rate of these birds in the interval from winter to the next breeding census, \(s_{d2}\). The variable \(X_{d2}\) included the survivors of this group plus those that dispersed from the natal territory between winter census and the next breeding season. We assumed that \(s_{d2}\) applied to these late departers as well. This enabled calculation of \(N_{d2}\), and thus \(s_{h2}\), using equations (8) and (9), substituting the \(s\) terms for the \(L\) terms of the equations. The winter census indicated the number of survivors for both tactics in the interval between fledging and winter census, \(X_{d1}\) and \(X_{h1}\). All birds that remained on the natal territory in this interval were included among the \(X_{h1}\), whether they remained or departed in the second interval, because we assumed that behavior in the second interval would not affect survival in the first. We then determined a constant \(c\), such that

\[
cs_{h2} = s_{h1} = X_{h1} / N_{h1} \tag{10}\]

and

\[
cs_{d2} = s_{d1} = X_{d1} / N_{d1}. \tag{11}\]
Thus we assume that, although the absolute survival rates might change, the ratio of the survival rates for the two tactics remained constant. Not unexpectedly, mortality was greater in the first interval, when the young had recently fledged, such that \( c = 0.94 \). We computed \( L_h \) and \( L_d \) as follows:

\[
L_h = \frac{X_{h2}}{N_h}, \tag{12}
\]

\[
N_h = X_{h2} + Y_{h2} + Y_{h1} - (X_{d2} + Y_{d2}/s_{h1}) - (X_{d2} + Y_{d2}) \tag{13}
\]

and

\[
L_d = X_{d2}/(N - N_h), \tag{14}
\]

where \( Y_{ab} \) is the number of deaths of those following tactic \( a \) in interval \( b \). The fourth term of equation (13) is necessary so that the fraction of birds that died on the natal territory before winter census, but would have departed after winter census had they survived, are counted under DAS instead of SAF. We assume that this fraction is the same among those who died in the first interval as those who survived.

3. The survival of first-year males in the winter census sample was 52\%, whereas it was 44\% for the study as a whole. Therefore, we calculated \( L_h \) and \( L_d \) in a third way that corrected for the unusually high survival of the birds in the winter census sample. Again, the approach taken was to determine a constant, \( z \), that could be multiplied by the survival values computed by the second method such that their relative values remained the same while absolute values increased sufficiently to produce the desired total survival. The value of this constant was 0.875.

Because males seldom inherit breeding status on their natal territory during their first year and because such vacancies could arise before a male chooses its tactic, we did not include the possibility of breeding on the natal territory at age 1 within either tactic. To determine how inheritance at age 1 could affect relative payoffs, we calculated additional estimates for all three methods, including such inheritance within SAF. This was done by adding the following term to equation (5):

\[
L_h \sum_{x=1}^{n} p_b^{x-1} m_x, \tag{15}
\]

where \( I \) equals the probability that a fledgling that is still alive and present on its natal territory at age 1 will have breeding rather than nonbreeding (helping) status.

**Emigration Assumptions**

In the above calculations, we assume birds that disappear died. Some of these birds presumably emigrated from the study area to become breeders elsewhere. Our study area includes the limits of the population to the north and west, and no additional populations exist in those directions, but other portions of the population occur immediately to the east and south of the study area. We therefore
derived a series of estimates of levels of emigration, based on observed rates of immigration of unbanded birds into the study area, as follows (see Walters et al. 1988 for details). (1) Assume that the number of immigrants equals the number of emigrants. Assume that emigrants are divided among fledglings, floaters, helpers, solitary males, and breeders, as are birds (banded and unbanded) that immigrate into groups within the study area (40%, 10%, 25%, 15%, and 9%, respectively). (2) Again assume that immigration equals emigration, but, because fledglings move farther than adults, assume that the proportion of each adult class among emigrants from the study area is half that of immigrants into groups within the study area, fledglings making up the remainder. This is our best estimate of emigration. (3) Assume that emigration equals immigration, and that all emigrants are fledglings. (4) Divide emigrants as in estimate 2, but assume that emigration is half immigration. (5) Divide emigrants as in estimate 2, but assume that emigration is twice immigration.

For each of the three methods of computing \( L_h \) and \( L_d \), we calculated the payoffs of the two tactics, assuming no emigration. We then computed a range of values around these estimates using the five emigration levels just described. The nature of the calculations precludes determining the statistical significance of a difference in payoffs for any single calculation. Therefore, for example, we could not determine whether mean fitness of those adopting DAS was statistically greater than that of those adopting SAF using the female mortality method and emigration level 2. However, for each of the three methods of computing \( L_h \) and \( L_d \), we determined whether the average difference in payoffs across emigration levels was statistically different from zero using two-tailed \( t \)-tests. We repeated this procedure for the additional measures of fitness described below.

Additional Measures of Fitness

Lifetime reproductive success often is an inappropriate measure of fitness for modeling selection. Under many population conditions an appropriate fitness measure in evaluating alternative life-history tactics is \( r \), the per capita population growth rate (Charlesworth 1980, p. 195; Partridge and Harvey 1988). Equations (3) and (5) may be condensed into standard \( l_x m_x \) schedules, where \( l_x \) is survival from fledging through age interval \( x \). We then calculated a second measure of fitness, \( r \), using the equation (Poole 1974, p. 19)

\[
I = \sum_{x=0}^{n} e^{-rx} l_x m_x. \tag{16}
\]

Because those that adopt DAS reproduce earlier than those adopting SAF, the former may have a selective advantage under some population conditions, even if they produce no more, or even fewer, young (Lewontin 1965). We therefore computed discounted lifetime reproductive success as a third measure of fitness. We discounted offspring by \( e^{-rx} \), thus weighting earlier offspring more, using a value of \( r \) calculated for the entire population, that is, combining the life-history schedules of both tactics. This procedure converted equations (3) and (5) as
follows for DAS:

\[ L_d T \sum_{x=1}^{n} e^{-rx} p_b^{(x-1)} m_x + L_d F p_t G \sum_{x=2}^{n} e^{-rx} p_b^{(x-2)} m_x \]

\[ + \sum_{i=2}^{n} L_d (1 - T - F) p_s^{(i-1)} S(1 - S)^{(i-2)} \sum_{x=i}^{n} e^{-rx} p_b^{(x-2)} m_x ; \] (17)

and for SAF:

\[ L_h \sum_{i=2}^{n} p_h^{(i-1)} (1 - B)^{(i-2)} B \sum_{x=i}^{n} e^{-rx} p_b^{(x-2)} m_x . \] (18)

**Observed Reproductive Success**

A critical assumption in our calculations is that reproductive success of breeders at a given age is independent of the tactic they used to become breeders. If helpers tend to occur on high-quality territories, as has been suggested by Stacey and Ligon (1987), then those adopting SAF may have higher reproductive success as breeders than do those adopting DAS. To determine whether our assumption of no difference between tactics was reasonable, we compared the observed reproductive success as breeders of the two types of males at each age for which data were available, using one-tailed t-tests.

**RESULTS**

Estimates of age-specific reproduction are given in figure 1, and estimates of other model variables are given in tables 1 and 2. In the first year survival of males practicing SAF was considerably higher than that of males practicing DAS, for all methods of calculation. The probability that males practicing DAS that survived to age 1 would be breeders (rather than floaters or solitary males) was only 43%. The annual probability that helpers would become breeders was 34%. The annual probability that solitary males would become breeders was much higher (64%). Helper survival was slightly higher than that of floaters or solitary males, but no higher than that of breeders. Breeding success was poor at young ages and improved with age until reaching an apparent plateau at about age 5.

Only 11 of 170 first-year males included in the winter census sample were discovered away from the natal territory. Thus calculation of survival rates during the first year for DAS in both the winter census and adjusted winter census methods is based on a small sample. The value for the adjusted winter census method nevertheless is intuitive. It is slightly lower than the estimate calculated using the female mortality method as one might expect, given that males adopting DAS move farther on average than females. Other variable estimates are based on reasonably large samples, except those pertaining to floaters (table 1). Because floaters are relatively uncommon, these variables have little effect on the calculations.
Fig. 1.—Age-specific reproduction of breeding males. Mean values and 95% confidence intervals are given. Sample size is indicated above each point.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>95% Confidence Interval</th>
<th>N</th>
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<tbody>
<tr>
<td>T</td>
<td>.43</td>
<td>.33-.54</td>
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</tr>
<tr>
<td>$p_b$</td>
<td>.77</td>
<td>.74-.79</td>
<td>1,032</td>
</tr>
<tr>
<td>$F$</td>
<td>.74</td>
<td>.65-.71</td>
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</tr>
<tr>
<td>$G$</td>
<td>.56</td>
<td>.50-.68</td>
<td>30</td>
</tr>
<tr>
<td>$p_f$</td>
<td>.67</td>
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<td>$1-T-F$</td>
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<td>.23-.43</td>
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<tr>
<td>$p_s$</td>
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<td>.55-.71</td>
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</tr>
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<td>$S$</td>
<td>.64</td>
<td>.54-.74</td>
<td>90</td>
</tr>
<tr>
<td>$B$</td>
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<td>.28-.40</td>
<td>274</td>
</tr>
<tr>
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<td>.73-.82</td>
<td>354</td>
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<td>$1-H$</td>
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<td>.80-.86</td>
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</tr>
<tr>
<td>$t$</td>
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<td>.22-.33</td>
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<tr>
<td>$M_0$</td>
<td>1.28</td>
<td>1.18-1.38</td>
<td>893</td>
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<tr>
<td>$I$</td>
<td>.08</td>
<td>.05-.11</td>
<td>241</td>
</tr>
</tbody>
</table>

Note.—Assuming no emigration. Adjustments for emigration are described in text.

Estimates of mean fitness for males employing the two tactics are nearly equal (table 3). Values calculated using the female mortality rate method are essentially identical, whereas the payoff of SAF slightly exceeds that of DAS when calculated by the winter census and adjusted winter census methods. However, the average difference between the two tactics across emigration levels was not statistically different from zero for these two methods (.05 < $P$ < .10). Gene-equivalents produced per lifetime calculated by the female mortality rate and adjusted winter census methods are close to 1.0, and $r$ is close to 0, as is expected in a stable-to-slightly-increasing population such as this. Values calculated by the
TABLE 2
SURVIVAL ESTIMATES FOR MALES ADOPTING
DAS ($L_d$) AND SAF ($L_h$) IN THE FIRST YEAR

<table>
<thead>
<tr>
<th>Method of Estimation and Variable</th>
<th>Estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female mortality rate:* $L_{d}$</td>
<td>.31</td>
</tr>
<tr>
<td></td>
<td>.52</td>
</tr>
<tr>
<td>Winter census:† $L_{d}$</td>
<td>.33</td>
</tr>
<tr>
<td></td>
<td>.64</td>
</tr>
<tr>
<td>Adjusted winter census:</td>
<td></td>
</tr>
<tr>
<td>$L_{d}$</td>
<td>.29</td>
</tr>
<tr>
<td>$L_{h}$</td>
<td>.56</td>
</tr>
</tbody>
</table>

NOTE.—Assuming no emigration. Adjustments for emigration are described in text.

* $N = 765$.
† $N = 170$ (total number of fledglings in sample). Only 11 of these were used to calculate $s_{d2}$.

winter census method are unrealistically high, reflecting the unusually high survival of fledglings in the sample used in this calculation. Results are similar for all three measures of fitness (table 3).

Extreme assumptions about emigration, specifically, that emigration does not occur or that emigration is twice immigration, lead to some disparity in the payoffs of DAS and SAF, but more reasonable assumptions result in less disparity. Examples of the effect of emigration assumptions on fitness calculations are given in figures 2 and 3. Note that the central four, more reasonable values cluster about the line of equal fitness when the female mortality rate method is used but cluster above the line, indicating greater fitness for those practicing SAF, when the adjusted winter census method is used. Results for other measures of fitness were identical.

The indirect component of fitness of helpers was calculated for only one fitness measure, lifetime gene-equivalents. The indirect component varied from 0.16 to 0.20 gene-equivalents, depending on method of calculation and migration assumptions. If subsequent studies indicate our exclusion of indirect fitness components to be in error, our results would be significantly altered. Those practicing SAF have slightly but consistently higher fitness than those practicing DAS if we include the indirect component, whereas the two types of males have nearly equal fitness when we exclude the indirect component. The indirect fitness component cannot be added directly to the direct fitness component because of the problem of double accounting (see above). However, since the reproduction of both types of males can be assumed to be equally augmented by assistance from helpers, the indirect fitness component can be added to the difference in direct fitness payoffs between the two tactics. Adding current indirect fitness would change this difference from 0.00–0.21 to 0.16–0.41 gene-equivalents per lifetime, de-
**TABLE 3**

**BEST ESTIMATES OF FITNESS OF MALES ADOPTING TWO LIFE-HISTORY TACTICS**

<table>
<thead>
<tr>
<th>Fitness Measure and Tactic</th>
<th>Method of Calculation</th>
<th>Female Mortality Rate</th>
<th>Winter Census</th>
<th>Adjusted Winter Census</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lifetime gene-equivalents:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SAF</td>
<td>1.08</td>
<td>1.34</td>
<td>1.17</td>
<td></td>
</tr>
<tr>
<td>DAS</td>
<td>1.08</td>
<td>1.13</td>
<td>.99</td>
<td></td>
</tr>
<tr>
<td>Lifetime discounted gene-equivalents:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SAF</td>
<td>.99</td>
<td>1.05</td>
<td>1.06</td>
<td></td>
</tr>
<tr>
<td>DAS</td>
<td>1.01</td>
<td>.92</td>
<td>.91</td>
<td></td>
</tr>
<tr>
<td>Per capita population growth rate:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SAF</td>
<td>.013</td>
<td>.049</td>
<td>.025</td>
<td></td>
</tr>
<tr>
<td>DAS</td>
<td>.016</td>
<td>.024</td>
<td>−.002</td>
<td></td>
</tr>
</tbody>
</table>

**Note.**—Best estimates assume emigration equals immigration and that 70% of emigrants are fledglings (departers; see text).

---

**Fig. 2.**—Lifetime reproductive success of males adopting SAF (helpers) and DAS (departers), measured in gene-equivalents, calculated using the female mortality rate method, for various migration assumptions. The square symbol represents the best estimate, which assumes that immigration equals emigration and that 70% of emigrants are fledglings. Circles give estimates for other migration assumptions described in the text. Line indicates equal payoffs of SAF and DAS.
FIG. 3.—Lifetime reproductive success of males adopting SAF (helpers) and DAS (departers), measured in gene-equivalents, calculated using the adjusted winter census method, for various migration assumptions. Format is as in fig. 2.

TABLE 4

OBSERVED AGE-SPECIFIC REPRODUCTION OF MALES FOLLOWING TWO LIFE-HISTORY TACTICS

| Tactic | SAF |  |
|--------|-----|--------|--------|--------|
|        | DAS | Total  | Natal  | Nonnatal|
| AGE    |     |        |        |        |
| 1*     | .46 (46) | .75 (24) | .75 (24) |        |
| 2      | 1.04 (48) | 1.19 (62) | 1.46 (37) | .80 (25) |
| 3      | 1.35 (40) | 1.37 (68) | 1.53 (38) | 1.13 (30) |
| 4      | 1.67 (30) | 1.74 (46) | 2.00 (25) | 1.43 (21) |
| 5      | 1.62 (16) | 1.90 (31) | 2.00 (18) | 1.77 (13) |
| 6–8    | 2.00 (16) | 2.00 (13) | 2.11 (9)  | 1.75 (4)  |

Note.—Reproduction is measured in fledglings produced and includes only paired breeders. Those practicing SAF are divided into those breeding on the natal territory and those breeding elsewhere. Sample sizes are given in parentheses.
* SAF and DAS differ at $P = .10$, one-tailed $t$-test.

Depending on method of calculation. For both the winter census and adjusted winter census methods, the average difference across emigration levels deviates significantly from zero when the indirect component is added ($P < .05$).

Including observed inheritance of the natal territory at age 1 increased fitness of those adopting SAF by only 0.03–0.05 gene-equivalents per lifetime. Because inheritance of the natal territory in the first year might occur before males were forced to choose between SAF and DAS in at least some cases, only some un-
known fraction of this value should be added to the difference in payoffs. We conclude that cases of inheritance of the natal territory at age 1 can be ignored in computing the relative payoffs of the two tactics.

Observed reproductive success of the two types of males as breeders differed significantly only at age 1 (table 4). However, if those practicing SAF were divided into those breeding on the natal territory and those breeding on adjacent territories following dispersal, those breeding on the natal territory consistently produced more young than males practicing DAS, whereas those breeding on nonnatal territories produced fewer young than males practicing DAS (table 4). Observed reproductive success of the two types of males differed at age 1 because all those practicing SAF were breeding on the natal territory. These results suggest that males adopting SAF tend to occur on high-quality territories but that our assumption of equal age-specific breeding success of the two types of males is reasonable, because high success of males adopting SAF when breeding on natal territories is balanced by poor success of such males when breeding on nonnatal territories.

DISCUSSION

_Evaluating the Demographic Model_

Our results provide the strongest empirical support yet that modeling the evolution of cooperative breeding as selection between alternative life-history tactics, as depicted in equations (3) and (5), is a valid approach. The tactics of the model match the observed behavior of the birds, and values of particular demographic parameters were consistent with the model. Specifically, we found survival advantages among those adopting SAF and low probabilities of successful dispersal and reproduction at an early age among those adopting DAS.

Of particular interest are variables pertaining to DAS, because these have not been directly measured in a cooperative breeder previously. Those variables that might be responsible for a reduced payoff of DAS relative to (noncooperative) species that do not employ SAF can be identified by comparison of values for red-cockaded woodpeckers to those in published reviews of avian demography (Ricklefs 1973; Clutton-Brock 1988; Welty and Baptista 1988, p. 400; Gill 1990, p. 411). Survival in the first year of males adopting SAF is extremely high relative to that of most noncooperative birds, being comparable to that of long-lived seabirds and gulls rather than small land birds. Survival in the first year is lower among males adopting DAS but is not particularly low compared with that of small noncooperative land birds. It is their probability of attaining breeding status given that they survive, not their survival, that is unusually low among males practicing DAS. The poor reproductive performance of those males that do attain breeding status at a young age is also striking. Such dramatic and prolonged improvement in reproductive success does not characterize small land birds generally, although it may be common among cooperative breeders (see, e.g., Woolfenden and Fitzpatrick 1984, p. 228).

The expected reproductive success at age 1 of a male adopting DAS thus is not much greater than zero, even if it survives. Although surviving males are
more likely to have breeding status by age 2 and subsequent ages if they adopt DAS than if they adopt SAF, this is balanced by greater survival among those that adopt SAF. By the age (5 yr) at which peak reproductive performance is reached, most (>80%) males employing SAF that survive are expected to be breeders. The end result is our primary finding: the fitness of individuals delaying dispersal and reproduction can indeed equal or exceed that of individuals that attempt independent reproduction at an early age. This is true even when indirect fitness benefits of helping behavior are not included in the payoff of SAF. This suggests that group formation can be explained by selection for SAF.

That SAF has as high a payoff as it does in red-cockaded woodpeckers is significant, because cooperative breeding is not highly evolved in this species, that is, SAF is not the dominant tactic. When SAF is the dominant tactic, considerable opportunity exists for the evolution of new adaptations that increase the payoff of SAF. Joint dispersal with siblings (Ligon and Ligon 1978, 1988; Koenig and Pitelka 1979), joint nesting (Mumme et al. 1988), and territory expansion by helpers to promote territorial budding (Woolfenden and Fitzpatrick 1978) are possible examples of such secondary adaptations.

Our results provide empirical support for modeling the evolution of delayed dispersal and reproduction in cooperative breeders as selection between alternative life-history tactics, but our use of average fitnesses likely oversimplifies the actual selection process. That the average payoffs of the two tactics are similar where both are common is reassuring, but whether the relative payoffs of the two tactics can account for their relative frequencies in the population is unclear from our data. First, our fitness measures may not be the correct ones. The measures we use are appropriate only under equilibrium conditions or under density independence (Charlesworth 1980, p. 195). If population regulation is density-dependent, selection will maximize the number of individuals in the age class in which regulation occurs, and fitness is a function of carrying capacity (Charlesworth 1980, p. 200). The population dynamics of red-cockaded woodpeckers are unusual (Walters et al. 1988; Walters 1991). Survival and reproduction are independent of population size, but the number of breeders is a strict function of the number of suitable territories present. Thus the number of breeders is remarkably constant, whereas there are density-independent fluctuations in the nonbreeding class due to gains from reproduction and losses to mortality and breeder replacement. Fitness is perhaps best measured by contribution to the breeder class, which may well be proportional to our primary measure of fitness, lifetime reproductive success.

Second, even if the fitness measures used are suitable, it is unlikely that selection can be accurately modeled in terms of average fitnesses. It is possible that the payoffs of the two tactics are constant, in which case one (apparently SAF in this case) would be selected at the expense of the other. However, it is much more likely that the payoffs vary, both over time and among individuals at a given time. Such variation could cause individuals to differ in which tactic produced the largest payoff and thus could enable both tactics to be maintained in the population. Although it may be a useful simplification to model selection for SAF in cooperative breeders using average fitnesses where differences in payoffs are
large, in species like the red-cockaded woodpeckers in which differences are small and both tactics are maintained, a more complex model is needed.

What possible sources of variation in relative payoffs of DAS and SAF exist? Frequency dependence is a distinct possibility. If choice of tactic is facultative, there are several other likely possibilities. Dominance rank might influence relative payoffs, because rank may affect the probability of inheriting a breeding position. The quality of the natal territory might affect payoffs (Stacey and Ligon 1987). Our data on observed reproductive success are consistent with this idea in indicating that helpers tend to inherit, and thus occur on, high-quality territories.

Finally, birds might be able to assess the degree of competition for breeding vacancies by observing the rate of intrusion of floaters and dispersing birds on their natal territory or by intruding on adjacent territories themselves. Indirect evidence suggests that choice of tactic is influenced by degree of competition. Few females adopted SAF, but, with only one exception, those that did were members of the two largest cohorts observed (table 5). The years in which female helpers occurred also were characterized by an unusually small number of unpaired males, another indication that competition for breeding vacancies among females was unusually great. The pattern among males is less clear. Although the ratio of those choosing SAF to those choosing DAS was greatest in the largest male cohort, the relationship between choice of tactic and degree of competition for breeding vacancies is less clear among other years (table 5).

Rather than try to more accurately model selection, we propose that another way to test the model depicted in equations (3) and (4) is to determine whether variation in choice of tactics is correlated with variation in relative payoffs. Comparing the sexes in their choice of tactics in red-cockaded woodpeckers is an example. In our study population, DAS prevails over SAF among females. We
can identify several differences between the sexes in values of model variables that decrease the payoff of SAF and increase the payoff of DAS for females relative to males. These differences appear sufficient to cause the payoff of DAS to exceed that of SAF. Mortality of breeding females is higher than that of breeding males (Walters et al. 1988). Increased turnover among breeders will increase $T$, the probability that those practicing DAS will acquire breeding status (and perhaps the survival of dispersers, $L_d$). This is evidenced by the shorter dispersal distances of females practicing DAS relative to males practicing DAS noted earlier.

The probability that helpers will acquire breeding positions, $B$, appears to be reduced in females relative to males as well. Conflicts over potential inbreeding are resolved by female, and not male, departure (Walters et al. 1988; Walters 1990), perhaps because males are behaviorally dominant to females. When a male inherits breeding status on its natal territory, its remaining female relatives leave. The converse does not occur. Therefore, for a female to inherit her natal territory, not only the breeding female but also the breeding male, if related to her, and any related male helpers must perish. Female helpers have a greater chance of becoming breeders in an adjacent site than do male helpers because female turnover is greater. This cannot compensate for the greatly reduced chance of inheriting the natal territory, however, since inheritance accounts for about half of the transitions from helper to breeder among males.

**Ecological Implications**

Our formulation of the payoffs of SAF and DAS differs from previous formulations (Vehrencamp 1979; Emlen 1982a; Stacey 1982; Wiley and Rabenold 1984; Woolfenden and Fitzpatrick 1984; Brown 1985, 1987) primarily in being more complex, that is, in making fewer simplifying assumptions. Differences in the models reflect implicit hypotheses about the ecological factors that drive demography. If it were the case that one formulation consistently fitted observed behavior better than the others, comparison of models could distinguish between ecological factors. The pattern does not appear to be this simple, however. Instead, the variables that are important differ among species, so that nearly as many models exist as species studied. This suggests that a complete formulation that includes all variables is the most appropriate general model and that such models have little potential to reveal much about the ecological basis of delayed dispersal and reproduction. The view that emerges is that a variety of combinations of demographic conditions can select for a single tactic, SAF. What matters is the sum, the fitness of those practicing SAF, not which aspects of demography contribute how much to this sum.

To evaluate the ecological basis of cooperative breeding, specific ecological models, rather than demographic models, are needed. We have developed such a model for red-cockaded woodpeckers, based on the ideas of Koenig and Pitelka (1981) and Stacey and Ligon (1987, 1991). If great variation in the quality of territories exists, an individual may be better off competing for high-quality territories, using SAF, and ignoring available low-quality ones, even if reproduction is thereby delayed. Suppose the presence of a single critical resource greatly
increases the quality of territories, so that individuals compete for territories with the resource, employing SAF, rather than accept a territory without it. Those territories that lack the resource remain unoccupied, although birds can survive and reproduce there. Elsewhere, we propose that the cavity tree cluster of red-cockaded woodpeckers is a resource of the type envisioned in this critical resource model (Walters 1990). Thus competition for territories with existing cavity trees produces a demographic regime under which SAF can be selected.

Two other related ecological models have also been proposed (Koenig and Pitelka 1981; Stacey and Ligon 1987, 1991). The models all depend on unusual relationships between fitness and habitat quality. These relationships result in an unusual degree of competition for particular breeding positions, a situation in which SAF is an effective tactic. It thus may be that a common tactic, SAF, is favored in several ecological circumstances. Researchers now face the tasks of determining which, if any, of the models are valid explanations of the evolution of delayed dispersal and reproduction in cooperative breeders and the relative frequency with which each applies.

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LITERATURE CITED


COOPERATIVE BREEDING IN WOODPECKERS


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