

## TEST OF THE ECOLOGICAL BASIS OF COOPERATIVE BREEDING IN RED-COCKADED WOODPECKERS

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**ABSTRACT.**—In many cooperatively breeding birds, the primary reason that helpers remain on the natal territory rather than disperse to breed independently may be to gain an advantage in competing for high-quality habitat. We hypothesized that cavities excavated in living pines, because they require much time to construct, are the critical determinant of habitat quality that has led to cooperative breeding in Red-cockaded Woodpeckers (*Picoides borealis*). These woodpeckers rarely colonize sites that lack existing cavities. To test our hypothesis we drilled cavities in 20 unoccupied sites. Eighteen were occupied subsequently, but none of 20 control sites were used. The manipulation added 12 new social units (breeding pairs or unpaired territorial males) to the population. New groups mostly comprised previous helpers and dispersing first-year birds. These results support our contention that variation in habitat quality dependent on the presence or absence of cavities is the ecological basis of group formation in Red-cockaded Woodpeckers. Cavity construction may be used to increase the number of groups in a population, and to prevent territory abandonment when bird-constructed cavities are lost. Received 3 October 1990, accepted 24 June 1991.

COOPERATIVE breeding refers to a social system found in birds and mammals in which some reproductively mature individuals (helpers) assist others in raising young (Brown 1978, 1987, Emlen and Vehrencamp 1983, Emlen 1992). Understanding the evolution of cooperative breeding involves two interrelated but distinct issues (Emlen 1982a, b, 1992, Brown 1985, 1987, Ligon and Stacey 1989): (1) determining what leads individuals to remain with their natal groups or form groups rather than disperse to breed independently; and (2) determining why such individuals engage in helping behavior such as feeding young. Altruism evolved through kin selection is an accepted explanation of helping behavior (issue 2; Emlen and Wrege 1988, 1989). In contrast, remaining in the natal group (issue 1) and thereby delaying reproduction and altering dispersal behavior generally is viewed as producing direct benefits to the individual under certain conditions (Emlen 1982a, Woolfenden and Fitzpatrick 1984, Brown 1985, 1987, Stacey and Ligon 1987).

Emlen (1982a) outlined two conditions under which remaining with the natal group may result in greater lifetime reproductive success than early dispersal and breeding. One condition involves a harsh, unpredictable environment. In

poor years, inexperienced birds reproduce poorly, so that living with the natal group is favored over independent reproduction. This hypothesis may apply to species that inhabit the dry regions of Africa and Australia (Reyer 1980, Emlen 1981, 1982a, Clarke 1984).

The second, perhaps more common condition has traditionally been termed habitat saturation, because it is thought to result from a shortage of vacancies in breeding habitat (Selander 1964, Brown 1969, Stacey 1979, Emlen 1982a). An apparent lack of unoccupied territories has been noted in many cooperative breeders (e.g. Selander 1964, Ridpath 1972, Woolfenden 1975, Ligon and Ligon 1978, Walters and Walters 1980, Zack and Ligon 1985, Koford et al. 1986), but not all (Rabenold 1985). In species to which the habitat-saturation hypothesis has been applied, helpers remain on their natal territory and compete for breeding vacancies on and in the immediate vicinity of the natal territory (stay-and-foray, abbreviated SAF), rather than dispersing after fledging to wander in search of a breeding vacancy (depart-and-search, DAS; Brown 1987). Those practicing SAF appear to have an advantage in competing for positions in their vicinity over those practicing DAS (Zack and Rabenold 1989), perhaps because they can monitor the availability of those positions much more effectively.

The demographic conditions under which SAF may be selected over DAS have been mod-

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eled by several authors (Vehrencamp 1979, Stacey 1982, Emlen 1982a, Wiley and Rabenold 1984, Woolfenden and Fitzpatrick 1984, Brown 1985, 1987, Stacey and Ligon 1987, Walters et al. 1992). The ecological conditions that produce habitat saturation, and thus the demography required for selection of SAF, are less well known. One hypothesis is that large variance in quality among breeding positions favors SAF (Koenig and Pitelka 1981, Stacey and Ligon 1987, 1991, Powell 1989, Emlen 1992). Variance in the quality of breeding positions may be dependent on effects of territory quality (Stacey and Ligon 1987, Powell 1989) or group size (Rabenold 1984) on fitness. According to this hypothesis, it benefits an individual to compete for a high-quality position, even if reproduction is thereby delayed, rather than accept a vacant low-quality position. High-quality positions are nearly always filled, and intense competition for high-quality breeding vacancies favors SAF.

*Red-cockaded woodpeckers.*—We have proposed that in the Red-cockaded Woodpecker (*Picoides borealis*), a single critical resource, the cavity-tree cluster, creates variation in habitat quality that results in selection for SAF among males (Walters et al. 1988, Walters 1990). In Red-cockaded Woodpeckers, groups typically consist of a breeding pair and one to three male helpers (Lennartz et al. 1987, Walters et al. 1988, Walters 1990). Helpers forego reproduction and assist the breeding pair with territorial defense, incubation, and brooding and feeding of young (Ligon 1970, Lennartz et al. 1987). In most cases, helpers assist on their natal territory and are related to one or both breeders (Walters et al. 1988). Males may practice either SAF or DAS, whereas nearly all females practice DAS (Walters et al. 1988, 1992, Walters 1990). Males practicing DAS leave their natal group before age 1 and disperse short to long distances. They may be breeders, unpaired males (territory but no mate), or floaters (no territory or mate) at age 1. Males practicing SAF remain in their natal group as helpers at age 1, and become breeders at some later age either on the natal territory or by dispersing a short distance, usually to an adjacent territory. Helpers rarely disperse long distances.

Red-cockaded Woodpeckers are unusual in excavating cavities in live pines, a process that takes at least 10 months, typically several years (Jackson et al. 1979). A territory includes a clus-

ter of cavity trees, and each bird occupies its own individual roost cavity. The group regularly adds to its existing cluster by excavating new cavities. One cavity, usually that of the breeding male and often the newest one, is used for nesting (Ligon 1970). We postulate that, although other factors may affect territory quality, the value of a set of cavities is such that the worst territories with existing suitable cavities are of substantially higher quality than the best territories that lack suitable cavities. It may benefit a bird to compete for territories with existing cavities, even if reproduction is delayed, rather than accept a territory without suitable cavities and construct them. Under these conditions, intense competition over existing cavity tree clusters may select for SAF. That Red-cockaded Woodpeckers rarely excavate new cavities to form new territories, but instead compete for breeding vacancies on territories with existing clusters, is consistent with the hypothesis (Walters et al. 1988, Doerr et al. 1989, Walters 1990).

To test our hypothesis, we constructed clusters of cavities in unoccupied habitat within a study area in the Sandhills of North Carolina. Cavities were constructed in abandoned territories containing old bird-constructed cavities, and in areas that contained neither birds nor old cavities. We predicted that addition of cavities would convert low-quality territories to high-quality territories, and would encourage territory occupancy.

#### METHODS

*Study area.*—We have studied the Red-cockaded Woodpecker population in a study area of greater than 110,000 ha in the Sandhills region of south-central North Carolina for 10 years. The locations of the approximately 225 woodpecker groups and their cavity trees within this study area are known, and over 95% of the individuals are banded with unique combinations of color bands. The experiment was conducted as part of a long-term study of population demography, during which all groups were censused each year, and all members identified from their color-band combinations. All young were banded each year as nestlings. Details of censusing and other methods are given in Walters et al. (1988).

The study area is forested primarily with second-growth longleaf pine (*Pinus palustris*), with scattered old-growth trees and ground cover dominated by wiregrass (*Aristida stricta*). Dense understories and midstories of one to several species of small oak (*Quercus* spp.) are common where fire suppression has oc-

curred. Red-cockaded Woodpecker cavities are primarily in longleaf pine, but some are in loblolly pine (*P. taeda*), which occurs as second growth on some old-field sites, and pond pine (*P. serotina*), which occurs along hillside drains and small creeks, and in pocosins along major streams. Detailed descriptions of the study area are found in Carter et al. (1983) and Walters et al. (1988).

*Cavity-construction technique.*—We designed a method of constructing cavities in live pine trees that produced minimum damage to trees, and cavities that closely imitated those constructed by the woodpeckers. Woodpecker-excavated cavities consist of a horizontal entrance tunnel through the sapwood into the heartwood, and a vertical cavity chamber within the heartwood. Man-made cavities imitated woodpecker-excavated cavities in the age and characteristics of the trees in which they were placed, their location in trees, their dimensions and their features (Copeyon 1990). The construction method was to drill the horizontal entrance tunnel first, then drill a second (access) tunnel above the entrance tunnel so that it descended at a steep angle to intercept the entrance tunnel. We then used smaller, flexible drill bits with extended shafts, inserted through the access tunnel, to scour out the cavity chamber within the heartwood (Copeyon 1990). We also constructed partial cavities (cavity starts), which consisted of the entrance tunnel and the beginnings of the cavity chamber.

*Experimental design.*—We identified 20 sites within the study area that appeared to be sufficient in size and foraging habitat quality to support a group, but contained no group or cavities. We paired these vacant sites according to habitat type, foraging-habitat quality and other characteristics, and used a coin toss to determine which member of each pair was to be an experimental site, and which a control. In experimental sites, we constructed two complete cavities and three cavity starts. We cleared hardwood understory and midstory, which are thought to inhibit Red-cockaded Woodpeckers from using cavities (U.S. Fish and Wildlife Service 1985), from the vicinity of trees in which cavities were constructed. We removed all vegetation greater than 0.75 m in height from a 5 to 10 m radius around each experimental tree with a chainsaw and hatchet. We located a set of trees suitable for cavities within each control site, but did not construct cavities in them. We did, however, clear hardwood understory and midstory from the vicinity of these trees. All sites were at least 0.5 km from existing cavity tree clusters.

In addition to vacant sites, we also constructed cavities in abandoned sites (i.e. in territories that contained cavities but no birds). We identified 20 abandoned clusters that appeared to contain primarily unsuitable cavities. Cavities may be unsuitable because they have been enlarged by other, larger species such as Red-bellied Woodpeckers (*Melanerpes carolinus*) or Pileated Woodpeckers (*Dryocopus pileatus*), or

because the bottom and walls of the vertical chamber have rotted. Seven of the 20 sites were abandoned at the beginning of our long-term study and, thus, had been abandoned at least seven to eight years prior to the construction. The others had been abandoned from one to seven years ( $\bar{x} = 5.2$  yr).

Again, we paired the clusters, and determined which would be experimental and which control by coin toss. We constructed two complete cavities and three cavity starts in each experimental cluster, and cleared hardwood understory and midstory from both experimental and control clusters.

We constructed cavities during February–March 1988 and November 1988–February 1989. Construction in three vacant and five abandoned sites was completed in the first interval, and the remaining construction in the second interval. Response to constructed cavities was assessed during the breeding season (April–July) of 1989.

*Monitoring of response.*—Red-cockaded Woodpeckers chip away at the sapwood around the cavities they use to form resin wells, from which sap flows. This sap flow prevents snakes from climbing to cavities (Rudolph et al. 1990). One can determine whether a particular cavity and, thus, a cluster of cavities is currently being used by Red-cockaded Woodpeckers based on the presence or absence of active resin wells (Jackson 1977). We determined the activity status of all clusters within the study area, including experimental and control clusters, at the beginning of the breeding season. We checked all active clusters every 9 to 11 days for nesting activity, and identified the birds in each cluster. We checked all inactive experimental sites monthly for new activity. We rechecked inactive abandoned control sites at the end of the breeding season. Because sap flow from resin wells is detectable for many months, this frequency of inspection permits detection of even brief occupation of cavities between visits. To determine whether vacant control sites became occupied, we checked the control trees and searched a circular area with a radius of 0.5 km around them at the beginning and end of the breeding season. Further details of methods used in monitoring active sites are found in Walters et al. (1988).

## RESULTS

Of 20 experimental sites, 18 (9 previously vacant and 9 previously abandoned) were occupied by July 1989. None of the 20 control sites were occupied. For both vacant and abandoned sites, the probability of such a disparity between experimental and control sites, under the null hypothesis that they are equally likely to be occupied, is 0.002 (matched-pairs test; Sokal and Rohlf 1973).

New social units formed in 10 sites, and 8

TABLE 1. Occupants of experimental sites.

| Occupant                                   | Type of site |           |
|--|--------------|-----------|
|  | Vacant       | Abandoned |
| New pair                                   | 2            | 4         |
| New unpaired male                          | 1            | 3         |
| Existing pair                              |              |           |
| Previous cluster occupied by new pair      | 1            | 0         |
| Previous cluster occupied by unpaired male | 0            | 1         |
| Previous cluster abandoned                 | 1            | 0         |
| Existing unpaired male                     |              |           |
| Previous cluster abandoned                 | 1            | 0         |
| Captured by existing pair <sup>a</sup>     | 3            | 1         |
| None                                       | 1            | 1         |

<sup>a</sup> A captured site is one used by an existing group that also continues to use its previous cluster.

were occupied by previously existing social units (Table 1). In two cases, new social units occupied the clusters abandoned by the birds that moved to the experimental site. Thus, the 18 occupied experimental sites produced a net increase of 12 social units. Seven of the new units were male-female pairs, and five were unpaired males. Nesting occurred in six experimental sites, and was successful in four.

The identities and previous histories of all members of the new social units were known. Of the 12 males, four (33%) were helpers from adjacent groups. Five (43%) others were individuals that presumably were practicing DAS (Table 2). Thus, most individuals were from those status classes that normally are involved in competition for naturally occurring breeding vacancies, indicating the birds responded to the

experimental sites as if they were suitable but unoccupied territories. Females ( $n = 7$ ) were dispersing young birds (57%; DAS strategy) or breeders from adjacent groups (43%). Breeding females frequently switch groups, generally moving only short distances, and breeding males occasionally move to adjacent clusters, usually after becoming unpaired (Walters et al. 1988). Long-distance movements by helpers or breeding males are extremely rare (Walters et al. 1988). Thus, the origin of two of the males occupying experimental sites is surprising (Table 2, last two entries). We assume unbanded immigrants into the study area are practicing DAS, as most long-distance movements of both sexes occur during the first year (Walters et al. 1988).

## DISCUSSION

The formation of new social units in response to constructed cavities contrasts to the infrequency of such events in the absence of manipulation. Our study area contains over 400 existing clusters of cavities, and over 200 existing social units, yet the rate of formation of new social units on new territories (vacant sites) is 0.75 units per year (Walters 1990), compared to 9 per year on 10 experimental sites. The rate of reoccupation of abandoned clusters is 9% per year (Doerr et al. 1989), but 90% per year in the experimental abandoned clusters.

The experiment provides direct evidence that potential habitat remains unoccupied because of lack of suitable cavities. There are unoccupied areas in which the birds could live, were they willing to roost in the open temporarily while excavating a cavity; however, they choose

TABLE 2. Prior status of members of new social units resulting from cavity construction. Status is for previous (1988) breeding season. Likely life-history strategy corresponding to each status class is given.

| Probable strategy/<br>prior status | Sex  |        |
|------------------------------------|------|--------|
|                                    | Male | Female |
| Depart-and-search                  |      |        |
| Fledgling                          | 3    | 3      |
| Floater, age 1                     | 1    | 1      |
| Unbanded                           | 1    | 0      |
| Stay-and-foray                     |      |        |
| Helper, adjacent cluster           | 4    | 0      |
| Other                              |      |        |
| Breeder, adjacent cluster          | 1    | 3      |
| Breeder, distant cluster           | 1    | 0      |
| Helper, distant cluster            | 1    | 0      |

not to occupy them. On territories with existing cavities birds sometimes roost in the open, occasionally for months, when their cavity is usurped by another species, or the number of group members exceeds the number of cavities. Secondary cavity nesters are often limited by availability of cavities, but Red-cockaded Woodpeckers make their own cavities and, thus, their limitation is self-imposed. Primary cavity nesters are expected to require trees suitable for cavity excavation, but not completed cavities.

*Implications for evolution of cooperative breeding.*—Our results support the general hypothesis that unusual variation in habitat quality selects for SAF in species characterized by habitat saturation. There are at least four variations of this habitat-quality model. In the marginal-habitat model of Koenig and Pitelka (1981), reproductive success falls sharply between suitable habitat and unsuitable habitat, and little marginal habitat exists between suitable and unsuitable habitat. Individuals cannot survive or breed in unsuitable habitat, whereas they can survive, but not breed, in marginal habitat. Under these conditions, suitable habitat is filled continuously, dispersal opportunities are limited, and SAF is favored over DAS. In noncooperative species, in contrast, dispersing individuals not able to locate a breeding vacancy in suitable habitat likely can locate in marginal habitat.

Stacey and Ligon (1987, 1991) proposed the benefits of philopatry model as an alternative to the marginal-habitat model. According to their model, SAF is adopted by individuals on high-quality territories in species in which unusually great variation in the quality of breeding positions exists. Although not explicitly suggested, it may also be that, when great variation in the quality of breeding positions exists, individuals compete for high-quality territories, using SAF, and ignore low-quality ones. This habitat-variance model is like the marginal-habitat model of Koenig and Pitelka (1981), except that habitat at the low end of the quality spectrum is low quality but suitable, instead of unsuitable, and the scarce intermediate habitat is suitable but of intermediate quality instead of marginal. The habitat-variance model may be identical to or distinct from the philopatry model, depending on how individuals assess and respond to habitat quality on the natal territory relative to the quality of other territories in the population.

The fourth variation is the critical-resource model we proposed for Red-cockaded Woodpeckers (Walters 1990). In our model, 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. In this situation, territories that lack the resource remain unoccupied. This model is like the habitat-variance model, except that territory quality has a discontinuous, rather than continuous, distribution.

The term habitat saturation might be restricted to the marginal-habitat model, the habitat-variance model, or both, because these models seem to best capture the spirit in which habitat saturation has usually been described. But habitat saturation might also be used in a general sense to describe the syndrome of intense competition over territories that are rarely vacant and, thus, could apply to all four models (Emlen 1992). Most discussions of habitat saturation refer to the demography common to all four models, rather than to the ecological basis of that demography. Thus, this general usage may be preferable. Certainly, we would not claim, for example, that all those who have advocated habitat saturation had the marginal-habitat model rather than the critical-resource model in mind.

Nevertheless, the ecological models are distinct. Although all may be correct in at least some cases, they are mutually exclusive in any particular case. In the marginal-habitat model, unoccupied habitat in which individuals could survive and breed successfully is rare or nonexistent, whereas in the other three models it exists, but is of relatively poor quality. The philopatry model predicts unusually high variation in reproductive success among occupied territories, whereas the other three models do not (Stacey and Ligon 1991).

We eliminated the marginal-habitat model for the Red-cockaded Woodpecker, because the experiment showed unoccupied habitat to be suitable. One might argue that birds cannot survive long enough in habitat lacking cavities to construct a new cavity, but this is unlikely, as they roost in the open for prolonged periods elsewhere. Of the remaining three models, we believe the critical-resource model seems most reasonable. That such a small change in the habitat as constructing two cavities and three cavity starts within a 60-ha territory produced such a

dramatic response argues against the habitat-variance model. That former helpers were frequent occupants of experimental sites argues against the philopatry model. Because the number of cavities added was small relative to the number present on most already occupied territories, our manipulation presumably was insufficient to create territories that are of unusually high quality relative to those already occupied. Therefore, if helpers remain on territories because of their exceptionally high quality, they should not be willing to leave them to inhabit the experimental sites.

It is difficult to evaluate the wider applicability of the different models. For most species, tests designed to distinguish the various possibilities are needed. The models are sufficiently similar that it will seldom be obvious which best fits a particular species. Even the marginal-habitat model is difficult to distinguish from the others in many cases. Species thought to fit the marginal-habitat model may instead fit the philopatry or habitat-variance model if vacant habitat is suitable (i.e. birds can live and reproduce there), but of low quality rather than unsuitable. For example the Florida Scrub Jay (*Aphelocoma coerulescens*) occupies a sharply defined habitat (scrub) and cannot occupy other habitats (Woolfenden and Fitzpatrick 1984). The species, thus, appears to fit the marginal-habitat model. However, Florida Scrub Jays are also highly sensitive to variation in quality within this scrub habitat. Specifically, reproductive success is greatly reduced in scrub that becomes tall and dense in the absence of fire. Birds do better, in terms of lifetime reproductive success, competing for recently burned scrub than occupying available unburned scrub, although they can live and breed in the latter (Fitzpatrick and Woolfenden 1986). Low-quality habitat is available, but the birds usually choose not to occupy it. Therefore, the species might also fit the habitat-variance or philopatry models.

Data analyzed by Stacey and Ligon (1991) indicate that variation in the quality of territories that are at least occasionally occupied is high in both Acorn Woodpeckers (*Melanerpes formicivorus*) and Green Woodhoopoes (*Phoeniculus purpureus*). This is consistent with the philopatry model, as they point out, and also the habitat-variance model, but not the marginal-habitat model.

The critical-resource model may be treated as a special case of the philopatry or habitat-vari-

ance models (Stacey and Ligon 1992). For many species, it is difficult to imagine a single critical resource sufficient to cause the kind of variation in territory quality required in the critical-resource model. This model may have limited application, perhaps to species like Red-cockaded Woodpeckers that invest considerable time and energy in constructing structures that can be inherited. Other possible examples include European badgers (*Meles meles*; Kruuk 1978) and pine voles (*Microtus pinetorum*; Fried 1987), which construct burrow systems, and Acorn Woodpeckers, which construct acorn storage granaries (Koenig and Mumme 1987). The partial success of experimental addition of acorn storage granaries to Acorn Woodpecker territories (Koenig and Mumme 1987:292) implies that the critical-resource model describes this species.

*Implications for conservation.*—The Red-cockaded Woodpecker is listed as a federally endangered species. The low rate at which new social units form and failure to occupy new habitat have been major obstacles to conservation (U.S. Fish and Wildlife Service 1985, Ligon et al. 1986). Our results indicate these problems to be a direct result of the basic biology of the species, and that cavity construction, in both vacant and abandoned habitat, can be used to overcome them (Copeyon et al. 1991). This offers hope that the continuing decline of the species (Ligon et al. 1986, Costa and Escano 1989) can be reversed.

A high rate of territory abandonment also has been a major management problem (Conner and Rudolph 1989, Costa and Escano 1989). Our results suggest that cavity construction in territories on which all cavities have been lost or have deteriorated will prevent territory abandonment. The U.S. Forest Service has acted on this suggestion on the Francis Marion National Forest in South Carolina by constructing cavities on territories where cavity trees were destroyed by Hurricane Hugo, with great success (R. Hooper, pers. comm.). This strategy should enable the population to recover more quickly from the devastation wrought by the storm by reducing the number of social units lost.

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