PATTERNS OF MORTALITY IN NESTS OF RED-COCKADED WOODPECKERS IN THE SANDHILLS OF SOUTHCENTRAL NORTH CAROLINA

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ABSTRACT.—Mean clutch size of Red-cockaded Woodpeckers (*Picoides borealis*) in the sandhills of southcentral North Carolina was 3.3 eggs, mean brood size was 2.3 nestlings, and the mean number of young fledged per successful nest was 1.9 fledglings. Many groups (9–25%, depending on year) did not nest at all. We estimated the total mortality rate of young for the entire nesting period to be 43% (range 31.8–49.5%). Total mortality was significantly higher for second nesting attempts than for first attempts. Also, nests initiated early in the nesting season had significantly lower mortality rates than those begun later in the season. Rates of whole brood loss were typical for temperate cavity-excavators, but partial brood loss was high. Whole brood loss usually occurred during incubation or soon after hatching. Of first nesting attempts, 21.6% failed to produce fledglings. Renesting was attempted by 13–61% of groups which failed, depending on year, and 0–50% of these attempts failed. Whole brood mortality rates increased significantly during 1980–1985. Whole brood loss appeared to be caused more often by other cavity-using species than by predators. Partial brood losses resulted from the loss of nestlings and the production of eggs that failed to hatch (at least 7.1%), including runt eggs (1.1% of all eggs). Losses of nestlings typically occurred between hatching and when young were 6 days of age, suggesting brood reduction. Mortality rates were significantly higher at this stage than for the preceding (incubation) and following (late nestling and early fledging) periods. Few nestlings were lost between banding (usually at age 5–10 days) and fledging checks (usually at ages 27–50 days, 1–14 days after fledging). Partial brood loss due to parasites appeared negligible, despite continuous use of individual cavities for as long as the duration of the study. *Received 15 July 1992, accepted 15 Sept. 1993.*

Understanding the population dynamics of endangered animals is critical to efforts to save these species. To describe population dynamics one must document demographic parameters (survival and fecundity) that characterize the natural population. Understanding population dynamics requires quantifying variation in reproduction and survival and identifying the environmental factors responsible for this variation. Based on knowledge of how environmental factors affect population dynamics, prescriptions for management to improve survival and reproduction can then be developed. In the present paper we analyze the population dynamics of the endangered Red-cockaded Woodpecker (*Picoides borealis*) based on data from a population in the sandhills of southcentral North Carolina. Data were collected over a six-year period from as many as 200 nests/

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yr. We present nest mortality rates and patterns of variation and discuss our results with respect to other studies of Red-cockaded Woodpecker (RCW) reproduction, population dynamics, and management.

<center>METHODS</center>

The study area (110,000 ha) is described in detail by Carter et al. (1983) and Walters et al. (1988). It contains three major areas of concentration of birds with intervening areas of lower bird density. The dominant vegetation is longleaf pine (*Pinus palustris*) with a predominantly scrub oak (*Quercus* spp.) understory. It contains about 550 adult birds which is about half the local RCW population (Walters et al. 1988). Nearly all (95%) of the birds were uniquely marked with color bands.

Data were collected from all known nests from 1980 through 1985. A typical Red-cockaded Woodpecker territory contains several cavity trees (Ligon 1970, 1971; Lay et al. 1971), referred to as a "cluster". At the beginning of each breeding season, each cluster was checked for evidence of active RCW use employing Jackson's (1977) criteria. Each active cluster was checked from early April until late July or until the group succeeded in producing at least one fledgling. In 1982 and 1983, clusters were checked for nesting activity approximately every 14 days; in all other years they were checked every nine days. All trees with active cavities were checked by tapping and scraping on the tree. When an adult appeared in the entrance, flushed from a cavity, or was observed in the vicinity, the tree was climbed and the cavity contents were recorded. If no nest was found in a cluster during the second cycle of nest visits, all active cavity trees were climbed and checked for evidence of nesting. In clusters where nesting attempts failed or where no nest was found, all active trees were climbed regularly, especially when adults were seen or heard nearby.

When a nest was found, the number of eggs, nestlings, and/or fledglings and their age and sex (if known) were recorded. The nest was then checked in each subsequent cycle of nest visits. Nestlings were aged using criteria in Ligon (1971). Each nestling, at age 4 days or older, was uniquely color banded, aged, and weighed.

For each nest in which young were banded, date of fledging (at age 26 days) was estimated, and fledging checks were conducted as soon after this date as possible. Nests were not revisited between banding and the fledging check. During the fledging check, the group was followed until its size was determined and all fledglings present were identified and sexed from crown patches. Male fledglings have a patch of red in their crown, whereas females do not (Ligon 1970). Any group missing a previously-banded nestling was followed at least twice to confirm that the bird had not fledged. Most fledging checks exceeded one hour; when birds were missing, total time spent following them frequently exceeded three hours. More than 99% of fledglings were detected using this procedure (Walters et al. 1988).

The young were aged when they were banded or during some other nest check during the nestling stage. For each nest, we calculated ages of eggs, nestlings and fledglings at the time of other checks of that nest by back- and fore-dating from the banding age or other known age. We adjusted some ages $\pm$ two days if the calculated clutch initiation day or hatch day did not match previous observations. For example, if only eggs and no nestlings were seen on a day calculated as nestling age 1 day, we set this date as age -1 day and adjusted all other ages for checks of that nest accordingly. The length of incubation is reported to be 10 or 11 days (Ligon 1970, Lennartz and Harlow 1979). For ease of calculations, we designated the day of hatch as age 0 days and the incubation period as -11 to -1 days. All eggs in a clutch are usually laid by day -11.

We considered clutches complete, and thus the clutch size known, if eggs in a nest were counted during the eleven days before hatch (-11 to -1 days) or if the count was consistent

on two checks during the egg stage. Since aging was done only for nestlings, age of nests lost during the egg stage could not be determined. Therefore, we did not include data from these nests in analyses of partial brood loss.

We considered eggs inviable if present in nests with nestlings at least three days old. Some eggs were noted as being smaller than normal, usually in comparison to the others present in the clutch. Eggs were not measured and records of small eggs are likely to be inconsistent among the observers. However, when these eggs were noted, it is probable that the size difference between the eggs was extreme. These eggs do not necessarily meet the criteria used in identifying runt eggs in studies of other species (see Koenig 1980a).

We described the patterns of mortality for eggs, nestlings, and fledglings following May-field's (1961, 1975) methods. The Mayfield method was appropriate during the period up to and including the date of banding, since nest check cycles were 14 da or fewer in all years (Johnson 1979). However, after banding, the nestlings usually were not visited again until after they fledged, a period that was typically 20 to 30 da.

We computed mortality rates and variances (Johnson 1979) for the periods preceding and following hatching for all nests, nests with known clutch sizes, and all successful nests. We compared mortality rates using Z-tests (Johnson 1979, Bart and Robson 1982). To look for seasonal trends, each nesting season was divided into two-week intervals starting with the first nest of the year. We also compared first nesting attempts to renests.

We examined whole and partial brood losses separately. Those nests that lost part of a brood initially and the remainder of the brood at a later time, were used in both sets of analyses. We calculated mortality rates for partial loss of a brood (PBL) using Mayfield's method (1961, 1975) for only those nests with known clutch sizes. Mortality rates for nest failure or whole brood loss (WBL) were also calculated by Mayfield's method. For each analysis, we divided the data into three age periods: incubation, 0–6 days, and 7+ days, to determine the timing of mortality.

RESULTS

Groups that contained at least one adult of each sex were considered potentially able to produce a nest. Increases in numbers of groups from one year to the next reflected increases in the area included in the study or the pairing of previously solitary male territory holders rather than formation of new territories (Table 1). The total number of nest attempts recorded and the number of fledglings produced were both highest in 1984 (Table 1). A highly variable proportion (9–25%; mean 17.4%) of potentially breeding groups failed to nest each year (Table 1).

Incubation commenced in mid-April, occurring as early as 13 April in 1985 and as late as 22 April in 1980. Date of last nest initiation was more variable among years and ranged from 23 May in 1985 to 3 July in 1983. Mean clutch size was consistently greater than three eggs (Table 2). Although data on renesting attempts were insufficient for detailed analysis, there was no obvious clutch size difference between first and second attempts. Mean clutch size was not correlated to the mean number of nestlings (Kendall Test for Independence, $\tau = 0.20$, $P = 0.72$) or fledglings ($\tau = 0.07$, $P = 1.00$) (Table 2). However, means for nestlings and fledglings were highly correlated ($\tau = 0.87$, $P = 0.016$).

TABLE 1
NUMBER OF GROUPS MONITORED[a], NESTS, FLEDGLINGS, AND GROUPS WITH NO RECORDED NEST

Year	Groups	Nests	Fledglings	Groups not nesting
1980	109	94	171	20
1981	183	160	294	28
1982	179	139	216	44
1983	185	157	223	38
1984	193	203	336	17
1985	203	176	243	36

[a] Increases in number of groups usually reflects the addition of groups not previously included in the sample.

Inviable eggs were frequently produced. In most years, 5–7% of all eggs seen were inviable by our definition (see above) (Table 3). In all years combined, 23 eggs (1.1% of all eggs seen) were reported to be runts. Of these, two were known to hatch, and 16 (69.6%) were inviable or were lost in a failed clutch. One female produced eight of these runt eggs in three attempts over two years.

Most nests were found before hatching occurred (Table 4). Many nests were found later in 1981 than in other years because the study area was expanded during the breeding season. Ninety-five percent of all nests observed were found by age 11.5 days. Median banding age for all years combined was 8 days ($s^2 = 15.9$), and 95% were banded by day 16 (Table 4). During 1981–1983, age of banding was higher than in the three other years because of longer nest check intervals. Half of all fledglings were seen within a week after fledging (by day 33), and 95% were seen by age 50 days.

TABLE 2
MEAN CLUTCH SIZE, MEAN NUMBER OF NESTLINGS PER NEST AND MEAN NUMBER OF FLEDGLINGS PER SUCCESSFUL NEST FOR NESTS OF KNOWN CLUTCH SIZE

Year	Mean clutch size	Mean number of nestlings	Mean number of fledglings
1980	3.18	2.27	1.98
1981	3.18	2.36	2.04
1982	3.20	2.26	1.86
1983	3.24	2.11	1.66
1984	3.47	2.53	2.07
1985	3.21	2.22	1.65
All years	3.27	2.31	1.88

TABLE 3

PERCENT OF INVIABLE EGGS

Year	Number of eggs seen	Percent inviable
1980	232	12.1
1981	262	6.5
1982	244	6.6
1983	370	8.6
1984	598	5.6
1985	469	5.5
All years	2175	7.1

Mortality Patterns

For all years combined, daily mortality rate for first attempts increased with the period of the season in which the nest was initiated (Kendall τ = 0.8, P = 0.05; Fig. 1). This pattern was not found in renesting attempts, but for both first and second attempts the variance of the mortality rate increased significantly over the season (τ = 0.8, P = 0.05). The percent of nests from which all eggs hatched and all young were observed as fledglings decreased steadily through the season (χ^2_3 = 15.3, P < 0.005; Fig. 2). In 1984, the only year with sufficient data for analysis, females of age 1 initiated first attempts significantly later in the season than females older than age 1 (χ^2_3 = 22.6, P < 0.005).

First nesting attempts had significantly lower mortality rates than second attempts in three years (Fig. 3; Z-test: P = 0.19, 0.0084, 0.25, 0.028, <0.0001, 0.15, for 1980–1985 respectively). The variances of these rates for second attempts differed by an order of magnitude from that of first

TABLE 4

MEDIAN AGES OF YOUNG WHEN NESTS WERE FIRST DISCOVERED, WHEN NESTLINGS WERE BANDED AND WHEN A FLEDGING CHECK WAS FIRST MADE

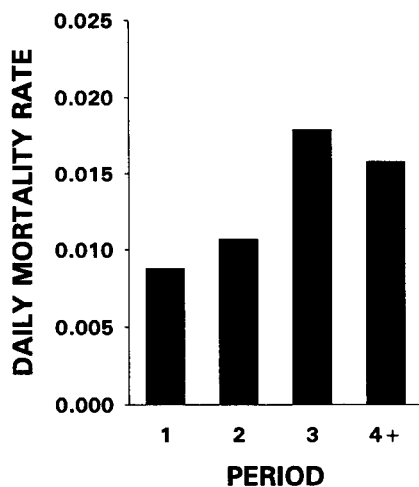| Year	Median age at discovery	Median age at banding	Median age at fledging check
1980	−7	7	28
1981	0	9	31.5
1982	−1	11	36.5
1983	−4	10	37
1984	−7	7	32
1985	−7	7	34
All years	−5	8	33

FIG. 1.   Daily mortality rates for first nesting attempts initiated in two-week periods during the nesting season (all years combined). Rates increase significantly throughout the season.
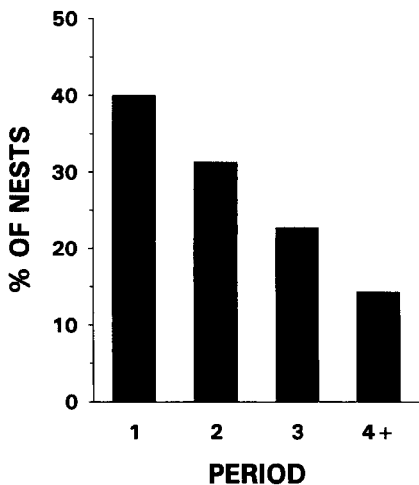

FIG. 2.   Percent of nests in which all eggs layed produced fledglings in nests initiated during two-week periods in the nesting season (all years combined).
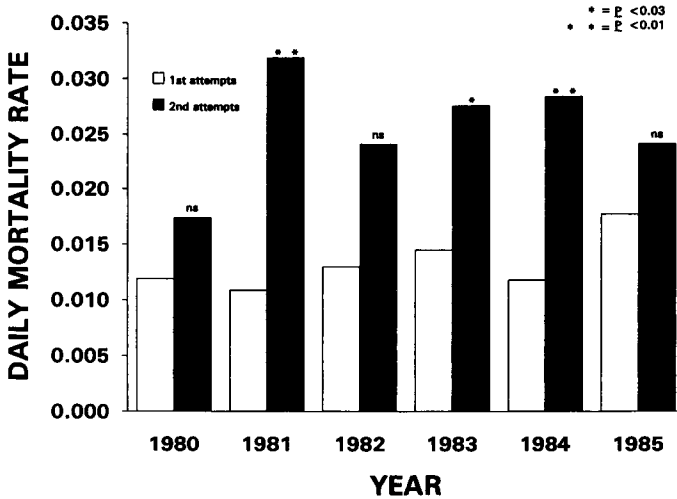
Fig. 3.   Daily mortality rates for first and second nesting attempts. Rates are significantly different in three years (Z-test).

attempts. Almost 34% of first attempts had no brood loss at all compared to 9.8% for second attempts. Differences between attempts were confounded with seasonal effects, since second attempts occurred later in the nesting season. Also, renests were attempted by groups that had already failed at their first attempt and thus may have been prone to failure, for example because they had poor territories or were comprised of young individuals.

For all years combined, 22.1% of the nests discovered experienced whole brood losses. Of first nesting attempts, 21.6% resulted in WBL (Table 5). The frequency of renesting was variable among years: 13.8–61.4% of failed first attempts were followed by renesting. One group nested three times in 1984, a phenomenon that had not been observed previously in RCWs. In this case, the first two nests both resulted in early (egg stage) WBL.

The daily rate of WBL, calculated by Mayfield's exposure method, was 0.0061 (s^2 = 0.00003); the rate for the entire nesting period was 0.2725. Rate of WBL increased significantly from 1980 to 1985 (Mann Trend Test, P = 0.008).

Most WBL occurred before nestlings were seen in the nest. For all nests, the nest mortality rate for the period following the first observation of nestlings was 0.08, and the observed frequency of nest loss for this same time period was 8%. This suggests that use of the Mayfield method

TABLE 5

PERCENT OF WHOLE BROOD LOSS (WBL) FOR FIRST NESTING ATTEMPTS, PERCENT OF FAILED
FIRST ATTEMPTS FOLLOWED BY RENESTING AND PERCENT WHOLE BROOD LOSS FOR
RENESTING ATTEMPTS

Year	Number of first attempts	Percent WBL of first attempts	Percent renesting	Percent WBL of renests
1980	89	14.6	38.5	0.0
1981	154	11.7	33.3	50.0
1982	135	21.5	13.8	50.0
1983	150	26.0	25.6	30.0
1984	177	24.9	61.4	44.4
1985	167	26.9	22.2	20.0
All yrs	872	21.6	33.0	35.5

for calculating this mortality rate was appropriate. The mortality rate for nests before nestlings were seen was 0.207, and the frequency of nest loss for such nests was 14.0%. We thus estimate that 20.7% of all (known and unknown) nests were lost before nestlings were seen and that 6.7% of all nests failed before their discovery. In the six years of the study, 929 nests were observed. We therefore estimate that in the six years 67 nests failed prior to detection. Thus, some nests counted as first attempts were actually second attempts, and some groups recorded as failing to nest actually nested but failed quickly. Still, at least 10 groups per year (116 total, 11% of all groups) did not nest.

We believe that very few nests were missed during the nestling period. In support of this assumption, one group in each of five years (0.5% of all known nests) was reported to have fledglings when no nest was previously reported.

Although causes of WBL were usually unknown, field notes associated with nest failures frequently mentioned other occupants in the nest cavity. Twenty-six WBLs (12.7% of all known WBL) occurred in cavities that later were reported to have another species nesting or roosting in them. Chief among these other species were southern flying squirrels (*Glaucomys volans*), Red-bellied Woodpeckers (*Melanerpes carolinus*), and Red-headed Woodpeckers (*M. erythrocephalus*). In addition, 15 groups that did not have a known nest (10.5% of non-nesting pairs) had cavities usurped by other species. Another known cause of WBL was fires that charred the tree and cavity (three known nest losses, one possible).

PBL mortality rates were significantly higher for the early nestling (0–6 days) age interval in each year (Fig. 4; Z-test, $P = 0.0084, 0.0014, <0.0001, <0.0001, <0.0001, <0.0001$, for 1980–1985 respectively). The
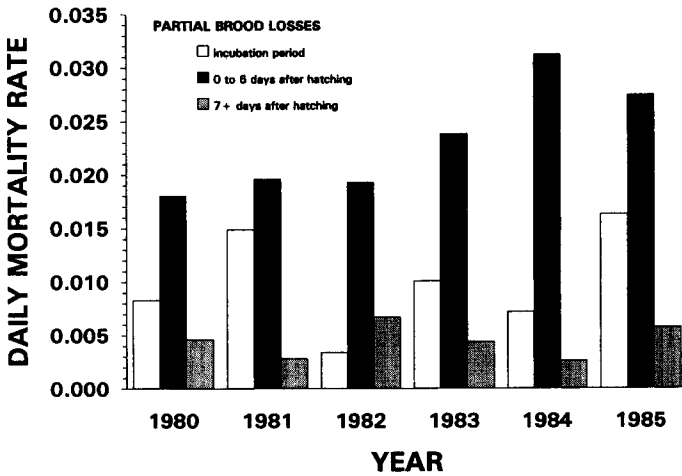
FIG. 4.   Daily mortality rates for different stages of nesting in different years. Rates are significantly higher in the early nesting period than in the incubation and late nestling periods in each year (Z-test, P = 0.01).

PBL mortality rate from the start of incubation to fledging was 0.2719 for all years combined. Annual variations in WBL and PBL mortality rates were not correlated (Kendall Test for Independence, τ = 0.552, P = 0.126). Although WBL mortality rates increased from 1980 to 1985, PBL rates did not (Mann Trend Test, P = 0.136). However, combining both types of mortality (PBL and WBL) the mortality rate per individual increased significantly from 1980 to 1985 (Mann Trend Test, P = 0.028).

DISCUSSION

The estimated number of nests missed (6.7%) is small considering the length of the nest-check intervals. The two years with longer (14-day) nest-check intervals did not have a higher frequency of missed nests than the years with nine-day cycles. This suggests that, for the purpose of recording nesting attempts, nest check cycles as long as 14 days are acceptable. However, for calculating mortality rates, nine-day cycles are more appropriate. By using this shorter cycle, rates can be calculated for specific stages of the nesting period, especially the incubation and early nestling stages. With the longer cycle the mortality rates for the stages within the nesting period are more likely to be biased.

The mean clutch size of 3.27 in our study agrees with values reported in other studies of this species (Ligon 1970, 1971; Baker 1971; Lennartz and Harlow 1979). The effects of age and timing of clutch initiation on

reproductive success observed are typical of avian species (Lack 1954, 1968; Perrins 1970; Clutton-Brock 1988). Age appears to have a particularly pronounced effect on reproductive success in Red-cockaded Woodpeckers, especially among males (Walters 1990). Groups in which the breeding male is only one year old account for many of the observed cases in which groups failed to nest (Walters 1990).

WBL and PBL are roughly equally important in brood mortality in RCWs, and their timing is similar as well. Both act primarily in the first half of the nesting period. Minimal losses occur after the young have reached age six days. The rate of WBL is comparable to other cavity-excavators in the temperate zone (Martin and Li 1992), but PBL is unusually high (total loss 27% versus 17% in other species, Nilsson 1986).

The loss of part of a brood early in the nestling stage, as occurs in Red-cockaded Woodpeckers, suggests brood reduction. This is thought to be an adaptation that enables the parents to match the number of young fledged to the food resources available (Lack 1954, 1968). It involves the early (soon after hatching) loss of the younger and smaller of asynchronously hatched nestlings, usually by starvation, when food is insufficient (O'Connor 1978). Significant partial brood loss is consistently observed in this species (Ligon 1970, 1971; Lay et al. 1971; Harlow 1983; Lennartz et al. 1987). In addition, incubation begins before the clutch is complete, hatching is asynchronous and nestling size discrepancies are typical (Ligon 1970, 1971; Walters et al., unpubl. data). That the early loss of RCW nestlings is due to starvation has yet to be verified, but all indirect evidence indicates that brood reduction is characteristic of the RCW. We detected no fluctuations in the extent of brood reduction indicative of adjustments to resource conditions.

Not all PBL can be attributed to brood reduction, however. Some was due to eggs failing to hatch. Since all eggs were not seen, and since inviable eggs could have been removed from the cavity before being noted by observers, 7.1% is undoubtably an underestimate of the percentage of eggs that failed to hatch.

Few studies of nesting in birds quantify hatching failure, usually noting only that some eggs are known not to hatch (e.g., Howe 1976, Murphy 1983). The percentages reported here do not, however, appear to be extreme. Custer and Pitelka (1977) reported 17.1% hatching failure in studies of Lapland Longspurs (*Calcarius lapponicus*) and Zach (1982) found hatching success to be 78–95% for Tree Swallows (*Tachycineta bicolor*).

Interestingly, there was no indication that parasites, a leading cause of PBL in many cavity-nesters (Nilsson 1986), were a significant mortality factor in RCWs. Ectoparasites were observed and recorded while handling the nestlings during banding. Although the same cavities are often used

for nesting for several years, only rarely did we observe significant nest infestations.

In addition to inviable eggs, some runt eggs were noted in RCW nests, as reported elsewhere (Ramey and Jackson 1979). Runt eggs may contribute to those eggs that fail to hatch. Among North American woodpeckers that are not cooperative breeders, the occurrence of runt eggs is uniformly low (range: 0–0.797%) (Koenig 1980b). For RCWs, Koenig (1980b) reported 1.33% of 75 eggs in museum collections were runts, a value similar to the (minimum) value reported here. Koenig (1980b) suggests that cooperative breeding may contribute to the overproduction of runt eggs in Acorn Woodpeckers (*Melanerpes formicivorous*). Our data provide additional evidence of a link between cooperative breeding and the production of runt eggs.

The presence of other occupants in former nest cavities indicates that loss of cavities to other species may be responsible for much WBL. Other species are known to usurp RCW cavities (Carter et al. 1989). In addition, destruction of RCW nests has been noted. Other bird species remove RCW eggs, and southern flying squirrels crush and possibly eat the eggs (pers. obs.). Because dead trees are easily destroyed by the frequent fires associated with this habitat and only RCWs construct cavities in live trees, Godfrey (1977) suggested that both secondary and other primary cavity nesters in pine savannas "rely" on RCWs to construct cavities. This could lead to unusually high levels of nest losses in RCWs compared to other cavity-excavators.

That most WBL occurred early in the nesting cycle suggests that nest desertion is a major cause of WBL (Ricklefs 1969). Frequent nest desertion might be related to the complex social system of this species. Lack of correlation between PBL and WBL suggests that starvation of young is not a major component of WBL. Loss of broods to predators such as snakes appears to be exceptionally infrequent, even for a cavity excavating species (Walters 1990). This presumably reflects the effectiveness of the pine resin barrier produced by the birds around their cavities (Rudolph et al. 1990).

Variation in reproductive output between years was a function of WBL and the proportion of groups that did not nest. Others also have noted that some potentially breeding groups of RCWs fail to nest (Hopkins and Lynn 1971, Wood 1983). Such events may be related to occupation of cavities by other species. However, variation in failure to nest was not correlated with variation in WBL, as it should be if usurpation of cavities during the nesting season was a factor in both. Instead, variation in failure to nest was correlated with variation in renesting. Years in which the highest proportion of groups nested also had the highest renesting rate

when broods failed (Kendall Test $P = 0.068$, Tables 1, 5). This suggests annual variation in reproductive effort. Perhaps individuals whose chances of success are low forego breeding when conditions are poor. One-year-old males have the lowest success rate of any age-sex class when they attempt nesting and also are most likely to fail to nest (Walters 1990).

The patterns observed suggest few opportunities to increase reproduction through management. One possibility is that WBL, and perhaps failure to nest, could be reduced by reducing usurpation of RCW cavities by other species. Some studies have suggested that frequency of cavity usurpation of RCW cavities is positively related to development of hardwood understory (Jackson 1978), others that it is related to availability of snags in the vicinity of the cluster (Harlow and Lennartz 1983). Everhart (1986) found no evidence for either relationship in our study area. Clearly, additional research is needed to determine whether reducing use of RCW cavities by other species can improve RCW reproduction. We are currently testing this hypothesis experimentally using metal plates (restrictors; Carter et al. 1989) that restrict access of some other species to RCW cavities at the cavity entrance.

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