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## INFLUENCE OF HABITAT AND NUMBER OF NESTLINGS ON PARTIAL BROOD LOSS IN RED-COCKADED WOODPECKERS

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**Abstract:** Partial brood loss in red-cockaded woodpeckers (*Picoides borealis*) was studied during 2 breeding seasons in eastern Texas. The timing of partial brood loss, group size, number of initial nestlings, number of birds fledged, and habitat characteristics of the group's cavity-tree cluster were examined for 37 woodpecker groups in loblolly- (*Pinus taeda*) shortleaf (*P. echinata*) pine habitat and 14 groups in longleaf (*P. palustris*) pine habitat. Partial brood loss occurred slightly more in the loblolly-shortleaf pine habitat than in the longleaf pine habitat, largely because nests in loblolly-shortleaf habitat initially contained more nestlings. There was a trend for more young to be fledged by groups of 4 and 5 adult woodpeckers than by groups with only 2 or 3 adult birds. Partial brood loss was greater in nests with 4 initial nestlings than in nests with 3 or fewer nestlings. Partial brood loss was always observed in nests that initially contained 4 nestlings. When nests contained 3 nestlings, partial brood loss was significantly greater in clusters where hardwood midstory was present than in clusters where hardwood midstory was minimal, consistent with the brood reduction theory. Red-cockaded woodpeckers typically

laid more eggs than they could possibly fledge young, lending support to the insurance egg hypothesis.

**Keywords:** red-cockaded woodpecker, brood reduction, partial brood loss, insurance egg hypothesis.

The adaptive significance of avian brood reduction proposed by Lack (1954) suggests that females lay as many eggs as they can successfully raise and fledge young during a favorable year when food resources are plentiful. If food becomes scarce during a particular nesting period, however, some young may be lost to starvation. Asynchronous hatching is believed to facilitate this phenomenon by placing younger, weaker nestlings at a competitive disadvantage relative to their older siblings. This strategy also ensures that if the brood needs to be reduced, the event will occur early in the nesting cycle when little investment has been made in the youngest nestlings (Lack 1954).

Several studies have failed to document a link between asynchronous hatching and adaptive brood reduction (reviewed in Ricklefs 2000b). Consequently, as many as 16 alternatives to Lack's (1954) brood reduction hypotheses have been introduced to explain why some species show asynchronous hatching and often tend to lay more eggs than can normally be raised to fledging (reviewed by Stoleson and Beissinger 1995). Two of these hypotheses state that both asynchronous hatching and associated partial brood loss are nonadaptive consequences of physiological constraints (e.g. hormonal control mechanisms, energy limitations) that force either early onset of incubation behavior or inconsistency in incubation bout duration (Stoleson and Beissinger 1995). Four hypotheses purport a selective advantage to immediate incubation with hatching asynchrony representing a mere epiphenomenon. An example from this hypothesis class is the egg viability hypothesis (Arnold et al. 1987) that suggests incubation begins prior to clutch completion due to decreasing hatchability of first laid eggs over time. Seven hypotheses state a potential adaptive role for asynchronous hatching during the nestling phase. An example is the insurance egg hypothesis (Stinson 1979), which proposes that birds will lay an extra egg to insure against the early death of a hatchling or egg that does not survive. The remaining 3 hypotheses point to potential adaptive roles at both the incubation and nestling phases. These include the nest failure (Clark and Wilson 1981) and adult predation hypotheses (Magrath 1988). The nest failure hypothesis predicts that incubation will

begin before clutch completion in species with high nest predation rates during the egg phase. Alternatively, in species with higher rates of nest predation associated with the nestling phase, incubation begins only after clutch completion. The adult predation hypothesis states that species with high incubation-associated predation rates should initiate incubation only after clutch completion to minimize incubation duration.

We examine partial brood loss in red-cockaded woodpeckers in an attempt to elucidate the possible adaptive significance of asynchronous hatching. In particular, our data are relevant to the brood reduction, egg viability, insurance egg, and nest failure hypotheses.

The red-cockaded woodpecker (*Picoides borealis*) is a cooperatively breeding species endemic to the southeastern United States. Clutch size ranges from 2 to 4 eggs with eggs being laid at approximately daily intervals (Ligon 1970). The incubation period is the shortest known among woodpeckers (10-11 days) and usually starts when the next to last egg is laid (Ligon 1970). Hatching is asynchronous with most young hatching the same day and 1 or 2 hatching the next day (Ligon 1971, LaBranche 1992). The usual nestling period is 26-29 days (Ligon 1971). Nest failure rates (total loss of eggs and/or nestlings) average about 20% throughout the species range (U.S. Fish and Wildlife Service 2000). Nest failures are primarily caused by nest predation, nest abandonment, and cavity kleptoparasitism and the failure rate is higher during egg laying than in the nestling stage (Sanders 2000, Conner et al. 2001a). Some partial brood loss results from nonviable eggs (LaBranche and Walters 1994). Some eggs may be infertile, or some may not hatch due to cessation of incubation by the group. As often occurs with asynchronous hatching, most partial brood loss in red-cockaded woodpeckers appears to occur fairly soon after hatching (LaBranche and Walters 1994). It may be that the last hatched nestling dies from starvation or its nest mates or parents may kill it. Regardless of the mechanisms involved in partial brood loss in this species, the specific timing of loss events and the influence of habitat characteristics are not completely known.

In this study, we examined partial brood loss in red-cockaded woodpeckers nesting in the Angelina and Davy Crockett National Forests in Texas. Schaefer (1996) found few correlations between reproductive success and habitat characteristics in an earlier study on red-cockaded woodpeckers in Texas. Nesting success and adult weight, however, were greater in loblolly-

shortleaf pine habitat than longleaf pine habitat. In the present study, we ask the following questions: (1) is there a specific time period when partial brood loss takes place within red-cockaded woodpecker nests, (2) do habitat characteristics influence partial brood loss, and (3) does the number of nestlings or adult group size affect partial brood loss?

## STUDY AREA AND METHODS

Nesting phenology and partial brood loss were studied at 51 different red-cockaded woodpecker cavity-tree clusters over 2 nesting seasons (19 April to 13 June 1999 and 26 April to 1 July 2000) on the Angelina (ANF; 31°15' N, 94°15' W) and Davy Crockett National Forests (DCNF; 31°21' N, 95°07' W) in eastern Texas. We collected data on different red-cockaded woodpecker groups each year. Prior to the beginning of each breeding season (29 March to 14 April), each cluster was checked for evidence of active cavity trees using Jackson's (1977a) criteria. Active clusters were checked from 14 April through 14 July for the presence of eggs and/or nestlings in 1999 ( $n = 35$ ) and 2000 ( $n = 16$ ).

Clusters were checked every 5 days for nesting activity. If an adult bird was observed flying from the cavity or was seen in the area, we inspected the cavity tree with a Tree-Top II Peeper Video system (Richardson et al. 1999). If no nest was found during that regular visit, all trees were examined again for possible nesting at the next check interval. Woodpecker group size was determined for each group during April and May each year by counting adult woodpeckers as they assembled in the morning to commence foraging or as they returned to their clusters in the evening prior to roosting.

Confirmed red-cockaded woodpecker nest cavities were checked on a 3-day cycle. Each cavity was monitored for number of eggs laid, number of eggs hatched, number of nestlings present, and any obvious nestling size differences. Nestling age was determined using criteria developed by Ligon (1971). Our federal U.S. Fish and Wildlife Service endangered species permit allowed us only to check nest cavities every 3 days after hatching. To ensure that we examined all of the first 22 days of the nesting cycle, the nestling checks were staggered. For example, if 1 nestling was discovered on day 2 after hatching, that nestling was then checked on day 5 of its life. The next nest was then placed in the day 3 or the day 1 nest check cycle. This ensured that we would have adequate samples from

each of the 22 days of the nesting period and would reduce our probability of missing any brood loss events. To prevent premature fledging that might result from nest disturbance we ceased nest inspections at day 22.

Habitat characteristics were measured within a 100-m radius around each nest tree using 4 100-m transects in the 4 cardinal directions in longleaf pine ( $n = 14$ ) and loblolly-shortleaf pine ( $n = 37$ ) habitats. Along each transect we measured habitat variables at 10-m intervals using an ocular tube. At each point we measured the percentage of herbaceous vegetation, woody material, monocots, bare ground, leaf litter, ferns, and canopy closure (see James and Shugart 1970). A 1-factor metric basal area prism was used to measure the basal area ( $m^2/ha$ ) of pine overstory at each nest tree and at 50-m and 100-m intervals in the cardinal directions. The height of midstory surrounding the nest tree was measured using a range/height finder. Midstory density was also visually estimated and placed into 1 of 3 ordinal categories: none to sparse, moderately dense, and dense to very dense. Within the 100-m radius, old-growth pines were counted as indicated by gnarly branching and flat-top crowns.

We used a 2-way analysis of variance (ANOVA) with interaction (year and group size as main treatment effects) to examine differences between years for clutch size, number of nestlings, and number of fledglings. During 2000, no groups had 4 or 5 group members causing empty cells for our 2-way ANOVA design. Therefore, our 3 nest productivity measures were compared using type IV contrasts for interaction and 1999 versus 2000 (dropping groups with 4 and 5 members), group size 2 versus 3 using all data, and group size 3 versus 4, 3 versus 5, and 4 versus 5 using only 1999 data.

Because Pearson correlation analysis of habitat variables indicated that most habitat variables were inter-correlated ( $P \leq 0.06$ ), only the measure of hardwood midstory and habitat type were retained for comparisons with nest productivity. Fisher's Exact Test was used to determine if habitat type (loblolly-shortleaf or longleaf) affected partial brood loss. We used a Kaplan-Meier product-limit survival estimator to compute and plot the estimate of the distribution of the survival times for nests. We grouped nests by number of nestlings at hatch and compared product-limit survival distributions with the log-rank test. Because the estimator indicated that the distributions differed among number of nestlings at hatch ( $\chi^2 = 31.41$ ,  $P = < 0.0001$ ), we used pair-wise log-rank tests to distinguish differ-

ences among number of nestlings at hatch. We used a Bonferroni's correction to adjust significance levels for multiple tests ( $n = 6$ ).

We examined partial brood loss (occurred or did not occur) using Cox regression (proportional hazards regression) to model the relationship between group size, midstory density index (sparse, moderate, or dense), and habitat type (longleaf or loblolly-shortleaf) within number of nestlings at hatch. The models were created using backward elimination. Only when the initial number of nestlings was 3 did any predictors remain in the model. An assumption of Cox regression is that the hazard ratio does not change over time. Pair-wise tests for trend over time (SAS Institute Inc. 1992:439) indicated that none of the time-dependent explanatory variables were significant ( $P > 0.10$ ). There was no evidence of an increasing or decreasing trend over time in the hazard ratio.

## RESULTS

Clutch size for 51 nests examined in 1999 and 2000 averaged 3.35 ( $\pm 0.12$  SE) eggs and brood size averaged 2.56 ( $\pm 0.13$  SE) young at the time of hatching. As nests progressed from eggs ( $n = 171$ ) to nestlings ( $n = 131$ ) and nestlings to fledglings ( $n = 104$ ), losses were apparent at each subsequent nest stage (Figure 1). Two entire broods were depredated during the study; 1 during the egg stage and the other during the nestling stage. More than 23% (40 of 171) of the eggs laid did not hatch and more than 20% (27 of 131) of nestlings did not fledge from nests. Four was the modal clutch size, whereas 2 nestlings and 2 fledglings were modes of later nesting stages (Figure 1).

Two-way ANOVAs with interaction (group size and year as main treatment effects) using type IV contrasts failed to detect any difference between years for clutch size and number of nestlings, any effect of group size on clutch size, number of hatchlings, or number of fledglings, or any significant interactions ( $P > 0.05$ ). Two-way ANOVA using type IV contrasts detected a significantly greater number of fledglings produced in 1999 than in 2000 (type IV contrast  $SS = 2.16$ ,  $F_{1,50} = 4.78$ ,  $P = 0.034$ ). Although not significant statistically, clutch size, the initial number of nestlings, and number of fledglings increased with increasing woodpecker group size (Figure 2).

Partial brood loss occurred in 35% (18 of 51) of the nests examined during the 2-y study. Of the clusters that lost nestlings, 72% (13 out of 18 nests) exhibited

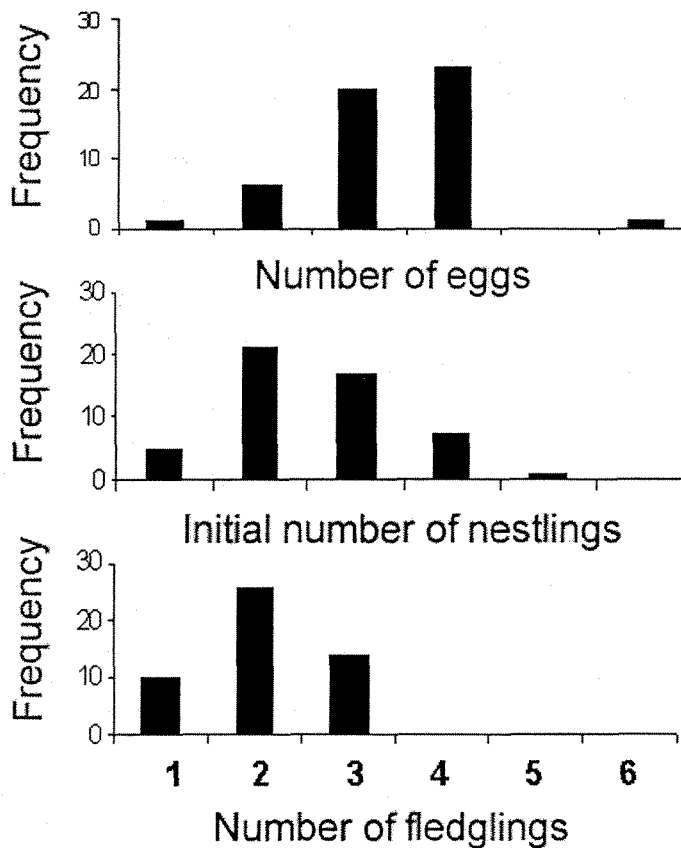


Figure 1. Frequencies of red-cockaded woodpecker nests with varying clutch sizes (top), initial brood sizes (middle), and fledglings (bottom) in eastern Texas.

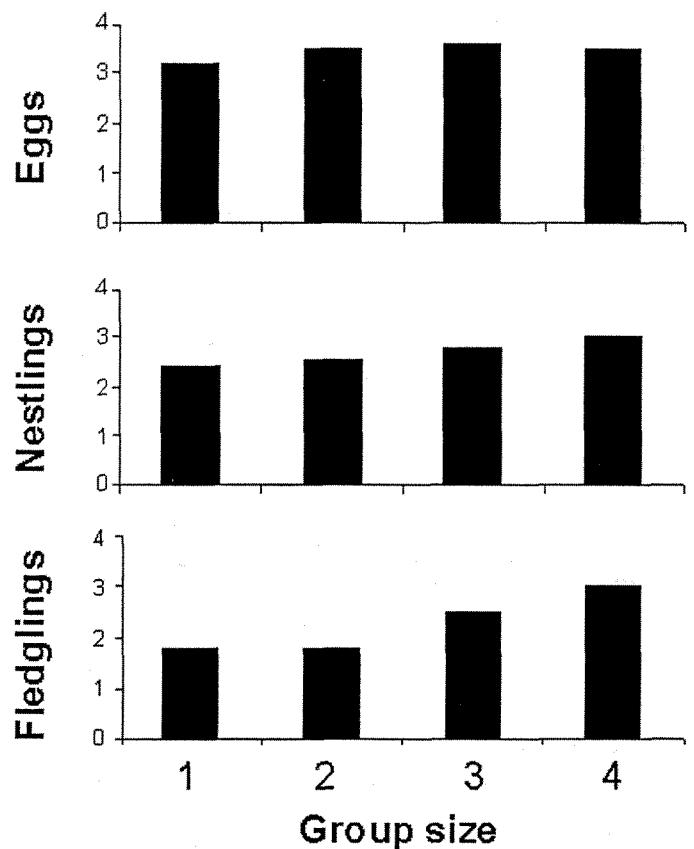


Figure 2. Average number of eggs, nestlings, and fledglings produced by groups of different sizes in eastern Texas.

partial brood loss before 9 days post hatching (Figure 3).

Brood size at hatching influenced nestling survival of red-cockaded woodpeckers in this population (Figure 4). Kaplan-Meier product-limit survival distributions were similar for nests with 3 or fewer nestlings (pair-wise log-rank test,  $\chi^2 \leq 4.44$ , adjusted  $P \geq 0.22$ ). The survival of chicks in broods of 4 was significantly lower than that of chicks in broods of 3 or less (pair-wise log-rank test,  $\chi^2 \geq 9.19$ , adjusted  $P \leq 0.014$ ). Nests starting with 4 nestlings always exhibited partial brood loss.

Slightly more partial brood loss occurred in loblolly-shortleaf pine habitat (43%, 16 of 37) than in longleaf pine habitat (14%, 2 of 14) (Fisher's Exact Test,  $\chi^2 = 3.73$ ,  $P = 0.099$ ). A Cox proportional hazards regression analysis was used to explore the relationships of habitat variables with partial brood loss. When only 1 nestling was initially present in the nest, no brood loss was observed. When the nest contained 2 or 4 nestlings

none of the habitat variables met the significance level to stay in the model ( $P = 0.10$ ). However, when nests had 3 nestlings in the cavity, midstory density remained in the model ( $\chi^2 = 5.17$ ,  $P = 0.02$ ). The hazard ratio (2.58) and sign of B (0.948) indicated that the estimated risk of partial brood loss increased with increasing values of midstory when nests initially contained 3 nestlings.

## DISCUSSION

LaBranche and Walters (1994) observed partial brood loss in 27% of red-cockaded woodpecker nests and suggested that it was unusually high when compared to other cavity nesting species. Sanders (2000) observed the highest frequency of red-cockaded woodpecker partial brood loss with 41% of the nests affected. LaBranche and Walters (1994) and Sanders (2000) also observed that most partial brood loss occurred during

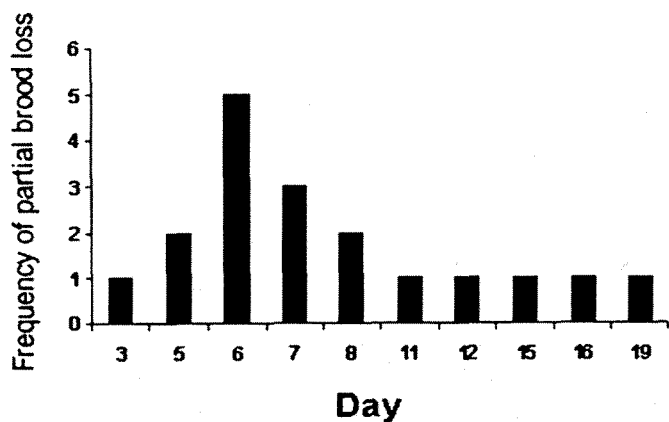


Figure 3. Bar graph showing days when partial brood loss occurred in nests and how many times brood loss occurred on that day for all nests.

the 8-day period post hatching. In support of Lack's (1954) brood reduction hypothesis, our observations suggest that it was the weakest nestling that disappeared. Similar to Sanders (2000) in South Carolina, we observed no aggression among nestlings during our frequent visits except for the variable positioning of nestlings when the inspection camera was inserted into the cavity. We frequently observed what appeared to be the weakest nestling lying at the bottom of the nest cavity, barely moving and likely suffering from malnutrition. Sanders (2000) suggested that starvation was likely a major mechanism of partial brood loss in red-

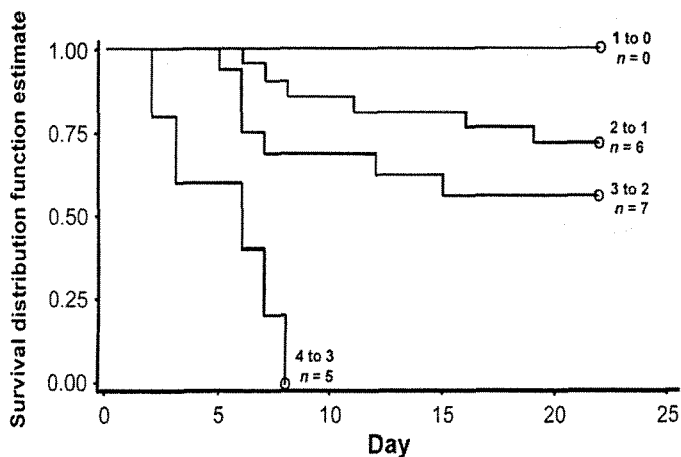


Figure 4. First time partial brood loss events (cumulative) on the Angelina and Davy Crockett National Forests in 1999 and 2000 for red-cockaded woodpecker nest cavities calculated using a Kaplan-Meier product-limit survival estimator. Brood loss events from clutches of 4 down to 1 are specified.

cockaded woodpeckers because the dying nestling lost or never gained weight. Because red-cockaded woodpeckers younger than 8 days did not appear to possess the necessary motor control to actively harm their nest mates, passive siblicide (more aggressive begging behavior) is most likely the mode of aggression that occurs in red-cockaded woodpecker nests.

The initial number of nestlings at hatching appeared to have the most influence on survival estimates. Nests with 1 nestling never exhibited brood loss, whereas nests with 4 nestlings always exhibited partial brood loss; no effect of habitat was detected. Partial brood loss was observed in some nests with 2 nestlings, but again it was independent of all habitat variables. However, partial brood loss was significantly related to excessive hardwood midstory when nests with 3 nestlings were present. It is in this last circumstance in which partial brood loss may possibly represent adaptive brood reduction given current ecological conditions.

These results suggest that partial brood loss in eastern Texas is very likely in broods with 4 nestlings. The question becomes "why ever lay more than 3 eggs if partial brood loss is always going to occur in such nests?" A clutch size of 4 may be a holdover from past ecological conditions. Historical habitat conditions in the southeastern United States were far different from conditions today. The larger expanses of contiguous open tracts of mature pines present in pre-Columbian times (Frost 1993) may have provided better foraging and nesting habitat, and clutch sizes of 4 may have been adaptive to those past ecological conditions.

However, the adaptive significance of a present day clutch size of 4 remains unclear. If the cost of egg production is relatively low and resource availability varies widely among years, the occasional rich resource year may allow the successful fledging of 4 or more nestlings from some nests. In fact, Walters (1990a) reported several instances of red-cockaded woodpeckers successfully fledging 4 nestlings and 1 instance where 5 were successfully fledged. In that population, clutch sizes of 4 may be adaptive. An additional possibility is that some extra egg production has virtually no cost and 4-egg clutches remain in the population as a result of a lack of selection pressure for their removal. As seen in this study, removing extra nestlings in early stages of development before substantial feeding effort is invested in them further minimizes costs.

The high number of 4-egg clutches in red-cockaded woodpeckers also appears to lend support to

Stinson's (1979) insurance egg hypothesis. The extra egg may serve as insurance against egg infertility or early nestling death. Our data indicate that the frequency of non-viable eggs might be quite high (also see Jordan 2003). The reason for so high a hatching failure rate is unclear and deserves further study. Initiation of incubation prior to clutch completion may be an attempt by red-cockaded woodpeckers to increase the hatch rate of first laid eggs (i.e. the egg viability hypothesis). Alternatively, early incubation initiation may actually be the cause of high hatching failure rates due to the early cessation of incubation as group members begin bringing food to nestlings. Due to permit restrictions, we did not mark eggs and do not know the laying order of eggs failing to hatch.

Initiation of incubation before clutch completion may also be influenced by the increased frequency of nest failures early in the egg stage of red-cockaded woodpecker nests (Conner et al. 2001a), supporting predictions of the nest failure hypothesis. However, support for this hypothesis is weak given the relatively low frequency of complete nest failures in this species and the fact that incubation is not initiated immediately after the first egg is laid.

Numerous previous studies indicate a strong relationship between the presence of a well developed hardwood midstory and cluster abandonment by red-cockaded woodpeckers (Conner and Rudolph 1989, Loeb et al. 1992, Conner et al. 1999). However, the reason why red-cockaded woodpeckers abandon clusters with encroaching hardwood midstory remains a matter of speculation (Conner and Rudolph 1989, Conner et al. 2001a). Hardesty et al. (1997b) and James et al. (1997) observed that high prey biomass was associated with a well developed herbaceous layer of grasses and forbs with minimal hardwood midstory, and that such habitat offers high quality reproductive conditions for red-cockaded woodpeckers. Collins et al. (2002) reported that arthropod density was greatest in an open pine stand and that vegetative structure was an important aspect in the foraging habitat of the red-cockaded woodpecker. In our present study, we documented an effect of hardwood midstory condition on reproductive fitness in broods with 3 initial nestlings. This observation has important implications for habitat management for this endangered species and emphasizes the need to reduce hardwood midstory and maintain open pine forest habitat where this species occurs.

In our study, partial brood loss occurred more

often in loblolly-shortleaf pine habitat than in longleaf pine habitat. Habitat structure in our longleaf study sites was very different from loblolly-shortleaf pine habitat. Typically, longleaf sites on the southern portion of the Angelina National Forest had a well developed herbaceous layer composed of grasses and forbs with less hardwood midstory as a result of frequent fire. Hardwood midstory was typically abundant in loblolly-shortleaf pine habitat in the northern portion of the Angelina National Forest and in all of the Davy Crockett National Forest.

This line of reasoning, however, at first appears inconsistent with observations by Schaefer (1996) in both habitat types. Schaefer (1996) observed slightly higher reproductive success in loblolly-shortleaf habitat than in longleaf pine habitat. A likely explanation for this difference is that there were very few southern pine beetle (*Dendroctonus frontalis*) infested pines available for woodpecker foraging in both forests during our study. Schaefer (1996) noted that southern pine beetle activity was significantly higher in loblolly-shortleaf pine habitat than in longleaf pine habitat during his study (see also Conner and Rudolph 1995b), which in turn was related to larger and more abundant prey, and a higher mean number of nestlings, fledglings, and adults in woodpecker groups. During the 2 years of the present study, southern pine beetle populations and activity were at extremely low levels (R. N. Conner et al., U.S. Forest Service, unpublished data).

In summary, partial brood loss in red-cockaded woodpeckers occurred primarily during the first 8 days post hatching. Partial brood loss in nests with 4 nestlings appears obligate in this population, whereas partial brood loss in nests with 3 nestlings appears to be related to hardwood midstory conditions surrounding the nest tree. In conjunction with previous research, our results suggest that red-cockaded woodpeckers have specific habitat requirements for both foraging and nesting and that high hardwood midstory density negatively impacts reproductive success.

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## LITERATURE CITED

- Arnold, T. W., F. C. Rohwer, and T. Armstrong. 1987. Egg viability, nest predation, and the adaptive significance of clutch size in prairie ducks. *Am. Nat.* 130:643-653.
- Clark, A. D., and D. S. Wilson. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. *Q. Rev. Biol.* 56:253-277.
- Collins, C. S., R. N. Conner, and D. Saenz. 2002. Influence of hardwood midstory and pine species on pine bole arthropods. *For. Ecol. Manage.* 164:211-220.
- Conner, R. N., and D. C. Rudolph. 1989. Red-cockaded woodpecker colony status and trends on the Angelina, Davy Crockett, and Sabine National Forests. U.S. For. Serv. Res. Pap. SO-250. 15pp.
- Conner, R. N., and D. C. Rudolph. 1995. Losses of red-cockaded woodpecker cavity trees to southern pine beetles. *Wilson Bull.* 107:81-92.
- Conner, R. N., D. C. Rudolph, R. R. Schaefer, D. Saenz, and C. E. Shackelford. 1999. Relationships among red-cockaded woodpecker group density, nestling provisioning rates, and habitat. *Wilson Bull.* 111:494-498.
- Conner, R. N., D. C. Rudolph, and J. R. Walters. 2001. The red-cockaded woodpecker, surviving in a fire-maintained ecosystem. Univ. Texas Press, Austin, 363pp.
- Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. *Tall Timbers Fire Ecology Conf.* 18:17-43.
- Hardesty, J. L., K. E. Gault, and H. F. Percival. 1997. Ecological correlates of red-cockaded woodpecker (*Picoides borealis*) foraging preference habitat use and home range size in northwest Florida (Englin Air Force Base). Final Res. Work Order 99. Nature Conserv. and Florida Coop. and Wildl. Res. Unit, Gainesville, Fl. 81pp.
- Jackson, J. A. 1977. Determination of the status of red-cockaded woodpecker colonies. *J. Wildl. Manage.* 41:448-452.
- James, F. C., C. A. Hess, and D. Kurfrin. 1997. Species-centered environmental analysis: indirect effects of fire history on red-cockaded woodpeckers. *Ecol. Appl.* 7:118-129.
- James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. *Aud. Field Notes* 24:727-736.
- Jordan, N. E., D. L. Otis, R. Costa, and S. A. Gauthreaux. 2003. Hatching failure and embryonic mortality within a red-cockaded woodpecker population in South Carolina *in* R. Costa and S. J. Daniels, eds. Red-cockaded woodpecker symposium IV, Hancock House Publishers, Blaine, Wa.
- LaBranche, M. S. 1992. Asynchronous hatching, brood reduction and sex ratio biases in red-cockaded woodpeckers. Ph.D. Thesis, North Carolina State Univ., Raleigh. 93pp.
- LaBranche, M. S., and J. R. Walters. 1994. Patterns of nest mortality in nests of red-cockaded woodpeckers in the Sandhills of south central North Carolina. *Wilson Bull.* 106:258-271.
- Lack, D. L. 1954. The natural regulation of animal numbers. Oxford Univ. Press, London, U.K. 252pp.



- Ligon, J. D. 1970. Behavior and breeding biology of the red-cockaded woodpecker. *Auk* 87:255-278.
- Ligon, J. D. 1971. Some factors influencing numbers of the red-cockaded woodpecker. Pages 30-43 in R. L. Thompson, editor. The ecology and management of the red-cockaded woodpecker. Bur. Sports Fish. and Wildl. and Tall Timbers Res. Stn., Tallahassee Fl.
- Loeb, S. C., W. D. Pepper, and A. T. Doyle. 1992. Habitat characteristics of active and abandoned red-cockaded woodpecker colonies. *South. J. Appl. For.* 16:120-125.
- Magrath, R. D. 1988. Hatching asynchrony in altricial birds: nest failure and adult survival. *Am. Nat.* 131:893-900.
- Richardson, D. M., J. W. Bradford, P. G. Range, and J. Christensen. 1999. A video probe system to inspect red-cockaded woodpecker cavities. *Wildl. Soc. Bull.* 27:353-356.
- Ricklefs, R. E. 2000. Lack, Skutch, and Moreau: the early development of life-history thinking. *Condor* 102:3-8.
- Sanders, F. J. 2000. Brood reduction and the insurance hypothesis as explanations for asynchronous hatching in red-cockaded woodpeckers. M.S. Thesis, Clemson Univ., Clemson, S.C. 84pp.
- SAS Institute Inc. 1992. SAS/STAT software: changes and enhancements. SAS Tech. Rep. P-229. SAS Institute Inc., Cary, NC 620pp.
- Schaefer, R. R. 1996. Red-cockaded woodpecker reproduction and provisioning of nestlings in relation to habitat. M.S. Thesis, Stephen F. Austin State Univ., Nacogdoches, Tx. 78pp.
- Stinson, C. H. 1979. On the selective advantage of fratricide in birds. *Evolution* 33:1219-1225.
- Stoleson, S. H., and S. R. Beissinger. 1995. Hatching asynchrony and the onset of incubation in birds, revisited: when is the critical period? Pages 191-270 in D. M. Power, ed. *Current Ornithology*, Vol. 12. Plenum Press, New York, NY.
- U.S. Fish and Wildlife Service. 2000. Technical/agency draft revised recovery plan for the red-cockaded woodpecker (*Picoides borealis*). U.S. Fish and Wildlife Service, Atlanta, Ga. 229pp.
- Walters, J. R. 1990. The red-cockaded woodpecker: a 'primitive' cooperative breeder. Pages 67-101 in P. B. Stacey and W. D. Koenig, eds. *Cooperative breeding in birds: long term studies of ecology and behavior*. Cambridge Univ. Press, Cambridge, U.K.

## LITERATURE CITED

- Arnold, T. W., F. C. Rohwer, and T. Armstrong. 1987. Egg viability, nest predation, and the adaptive significance of clutch size in prairie ducks. *Am. Nat.* 130:643-653.
- Clark, A. D., and D. S. Wilson. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. *Q. Rev. Biol.* 56:253-277.
- Collins, C. S., R. N. Conner, and D. Saenz. 2002. Influence of hardwood midstory and pine species on pine bole arthropods. *For. Ecol. Manage.* 164:211-220.
- Conner, R. N., and D. C. Rudolph. 1989. Red-cockaded woodpecker colony status and trends on the Angelina, Davy Crockett, and Sabine National Forests. U.S. For. Serv. Res. Pap. SO-250. 15pp.
- Conner, R. N., and D. C. Rudolph. 1995. Losses of red-cockaded woodpecker cavity trees to southern pine beetles. *Wilson Bull.* 107:81-92.
- Conner, R. N., D. C. Rudolph, R. R. Schaefer, D. Saenz, and C. E. Shackelford. 1999. Relationships among red-cockaded woodpecker group density, nestling provisioning rates, and habitat. *Wilson Bull.* 111:494-498.
- Conner, R. N., D. C. Rudolph, and J. R. Walters. 2001. The red-cockaded woodpecker, surviving in a fire-maintained ecosystem. Univ. Texas Press, Austin, 363pp.
- Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. *Tall Timbers Fire Ecology Conf.* 18:17-43.
- Hardesty, J. L., K. E. Gault, and H. F. Percival. 1997. Ecological correlates of red-cockaded woodpecker (*Picoides borealis*) foraging preference habitat use and home range size in northwest Florida (Englin Air Force Base). Final Res. Work Order 99. Nature Conserv. and Florida Coop. and Wildl. Res. Unit, Gainesville, Fl. 81pp.
- Jackson, J. A. 1977. Determination of the status of red-cockaded woodpecker colonies. *J. Wildl. Manage.* 41:448-452.
- James, F. C., C. A. Hess, and D. Kurfrin. 1997. Species-centered environmental analysis: indirect effects of fire history on red-cockaded woodpeckers. *Ecol. Appl.* 7:118-129.
- James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. *Aud. Field Notes* 24:727-736.
- Jordan, N. E., D. L. Otis, R. Costa, and S. A. Gauthreaux. 2003. Hatching failure and embryonic mortality within a red-cockaded woodpecker population in South Carolina *in* R. Costa and S. J. Daniels, eds. Red-cockaded woodpecker symposium IV, Hancock House Publishers, Blaine, Wa.
- LaBranche, M. S. 1992. Asynchronous hatching, brood reduction and sex ratio biases in red-cockaded woodpeckers. Ph.D. Thesis, North Carolina State Univ., Raleigh. 93pp.
- LaBranche, M. S., and J. R. Walters. 1994. Patterns of nest mortality in nests of red-cockaded woodpeckers in the Sandhills of south central North Carolina. *Wilson Bull.* 106:258-271.
- Lack, D. L. 1954. The natural regulation of animal numbers. Oxford Univ. Press, London, U.K. 252pp.

- Ligon, J. D. 1970. Behavior and breeding biology of the red-cockaded woodpecker. *Auk* 87:255-278.
- Ligon, J. D. 1971. Some factors influencing numbers of the red-cockaded woodpecker. Pages 30-43 in R. L. Thompson, editor. The ecology and management of the red-cockaded woodpecker. Bur. Sports Fish. and Wildl. and Tall Timbers Res. Stn., Tallahassee Fl.
- Loeb, S. C., W. D. Pepper, and A. T. Doyle. 1992. Habitat characteristics of active and abandoned red-cockaded woodpecker colonies. *South. J. Appl. For.* 16:120-125.
- Magrath, R. D. 1988. Hatching asynchrony in altricial birds: nest failure and adult survival. *Am. Nat.* 131:893-900.
- Richardson, D. M., J. W. Bradford, P. G. Range, and J. Christensen. 1999. A video probe system to inspect red-cockaded woodpecker cavities. *Wildl. Soc. Bull.* 27:353-356.
- Ricklefs, R. E. 2000. Lack, Skutch, and Moreau: the early development of life-history thinking. *Condor* 102:3-8.
- Sanders, F. J. 2000. Brood reduction and the insurance hypothesis as explanations for asynchronous hatching in red-cockaded woodpeckers. M.S. Thesis, Clemson Univ., Clemson, S.C. 84pp.
- SAS Institute Inc. 1992. SAS/STAT software: changes and enhancements. SAS Tech. Rep. P-229. SAS Institute Inc., Cary, NC 620pp.
- Schaefer, R. R. 1996. Red-cockaded woodpecker reproduction and provisioning of nestlings in relation to habitat. M.S. Thesis, Stephen F. Austin State Univ., Nacogdoches, Tx. 78pp.
- Stinson, C. H. 1979. On the selective advantage of fratricide in birds. *Evolution* 33:1219-1225.
- Stoleson, S. H., and S. R. Beissinger. 1995. Hatching asynchrony and the onset of incubation in birds, revisited: when is the critical period? Pages 191-270 in D. M. Power, ed. *Current Ornithology*, Vol. 12. Plenum Press, New York, NY.
- U.S. Fish and Wildlife Service. 2000. Technical/agency draft revised recovery plan for the red-cockaded woodpecker (*Picoides borealis*). U.S. Fish and Wildlife Service, Atlanta, Ga. 229pp.
- Walters, J. R. 1990. The red-cockaded woodpecker: a 'primitive' cooperative breeder. Pages 67-101 in P. B. Stacey and W. D. Koenig, eds. *Cooperative breeding in birds: long term studies of ecology and behavior*. Cambridge Univ. Press, Cambridge, U.K.