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Genetic Monogamy in Carolina Wrens (*Thryothorus ludovicianus*)

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Molecular comparisons have shown that socially monogamous passerines often have mixed reproductive strategies (Birkhead and Møller 1992, 1996). Pairs often cooperate in raising a brood, but each sex may pursue additional extrapair matings (e.g. Westneat 1987, Morton et al. 1990, Kempenaers et al. 1992). Further, females of some species lay eggs in nests of conspecifics (i.e. intraspecific brood parasitism, ISBP; reviewed in Hughes 1998).

Although considerable intra- and interspecific variation has been found in rates of extrapair paternity (EPP), causes for that variation remain unclear and additional data are warranted (Petrie and Kempenaers 1998). Further, few studies have been conducted on temperate-zone species that defend a territory and maintain a pair bond year round. In this study, we use multilocus DNA fingerprinting to examine paternity and intraspecific brood parasitism in Carolina Wrens (*Thryothorus ludovicianus*), a socially monogamous species that maintains a year-round pair bond and territory (Haggerty and Morton 1995). In addition, we report on breeding synchrony in Carolina Wrens because it is an ecological factor that may be related to paternity (Møller and Ninni 1998).

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Methods.—The study was conducted between March and August, 1996 and 1997, on a 43 ha mixed hardwood forest on the Tennessee Valley Authority reservation in Muscle Shoals, Colbert County, Alabama (34°49'N, 87°38'W). The overstory and understory are dominated by hackberry (*Celtis laevigata*) and privet (*Ligustrum vulgare*), respectively. During most of the breeding season, the ground-cover vegetation is dominated by honeysuckle (*Lonicera japonica*), poison ivy (*Rhus radicans*), and Virgina creeper (*Parthenocissus quinquefolia*).

Nest boxes were provided in late winter (5–6 per territory) and were readily used by Carolina Wrens (Haggerty and Morton 1995). Adults were captured near their nests with mist nets and approximately 30 to 100 μL of blood was collected from the brachial vein, stored in phosphate buffered saline/EDTA buffer (1996) or a lysis buffer (1997) and refrigerated. Blood samples from nestlings were collected in a similar way when they were 5 to 8 days old (hatching day = day 0). Adults were marked with a unique combination of colored leg bands and a U.S. Fish and Wildlife aluminum band. Parents caring for nestlings were the putative parents. Most adults had been previously banded as part of a long-term population study that began in 1988 (Haggerty and Morton 1995). Age (i.e. number of breeding years on study area) for adults that were fingerprinted ranged from 1 to 5 years ($\bar{x}$ = 1.6).

A 50 × 50 m grid system was established to help calculate size of the study area and to determine pair density. The 1996 and 1997 breeding-pair densities were 4.2 individuals/10 ha and 7.9/10 ha, respectively. A breeding-synchrony index was calculated for each year (Kempenaers 1993).

Multilocus DNA fingerprinting was conducted following the protocol of Loew and Fleischer (1996) using the Jeffreys 33.15 probe (Jeffreys et al. 1985). *Hae*III digested DNA of nestlings was usually placed in lanes between their putative parents for ease of scoring. Resulting autoradiographs were scored by counting number of fragments in a nestling's lane that were attributable to either or both parents profiles, and the number that were not (i.e. novel fragments). Pairwise band-sharing coefficients (S) were calculated according to Lynch (1991). A total of 84 offspring and 32 putative parents from 23 nests (i.e. a total of 116 individuals) were fingerprinted. Seven pairs were scored for two nests and nine pairs for only one nest. All offspring were fingerprinted for 16 of the 23 nests, but eight nestlings in seven nests were not analyzed because DNA was degraded or some other technical problem. Mean number of fragments per individual profile was 13.3 ± SD of 3.8 (range 6 to 24). Only fragments above about 3 kb were scored; hence, the smaller than normal number of fragments per profile. Typically, fragments below 3 kb were less variable than larger ones and they added little or no information to estimates of relatedness.

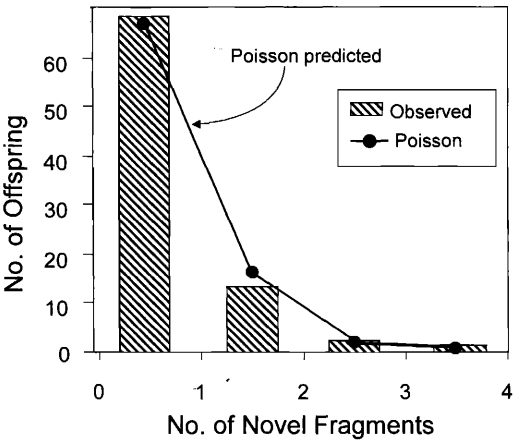

FIG. 1. Frequency of novel fragments among Carolina Wren offspring compared to their putative parents. Bars represent the observed frequencies. The line represents the theoretical distribution calculated from a Poisson distribution on the basis of mean number of fragments (0.238, n = 84) from nestlings with fewer than four novel fragments.

Results.—The synchrony indices for 1996 and 1997 were 17.7% ± 10 (n = 11 nests, 5 females) and 14.3% ± 11.0 (n = 39 nests, 19 females), respectively.

All DNA fragments found in offspring profiles were also found in the parent's profiles for 68 of the 84 offspring. For 13 offspring, we found one novel or nonattributable fragment. For two offspring, we found two novel bands and for one we found three. Mean number of novel fragments was 0.238 ± 0.55, corresponding to a mutation or artifact rate of 0.019 per fragment/generation. The distribution of novel fragments matches a Poisson expectation, on the basis of a mean of 0.238 (n = 84 profiles; Fig. 1). Because that match suggests that mutation alone can explain the extra fragments, we concluded, following the rationale of Westneat (1990), that there were no extra-pair fertilizations (EPFs) in our sample.

The mean value of S calculated for the 16 pairs of parents was 0.225 ± 0.13, which did not differ significantly from 11 random pairwise S values ($\bar{x}$ = 0.24 ± 0.1; t = 0.23, P = 0.82 [or Mann-Whitney U = 82.0, P = 0.77]). The predicted mean S for first-order relatives (R = 0.5) was 0.59 (equation 22 of Lynch 1991). Based on the level of background band-sharing, the probability of assigning parents incorrectly (ISBP) was 5.9×10^{-6}, whereas the probability of assigning the male parent incorrectly (EPF) was 1.9×10^{-4} (Bruford et al. 1998). The mean value of S for 84 comparisons of female parents and offspring was 0.52 ± 0.13, whereas S for male parents and offspring was 0.55 ± 0.11 (Fig. 2). The plot of S against

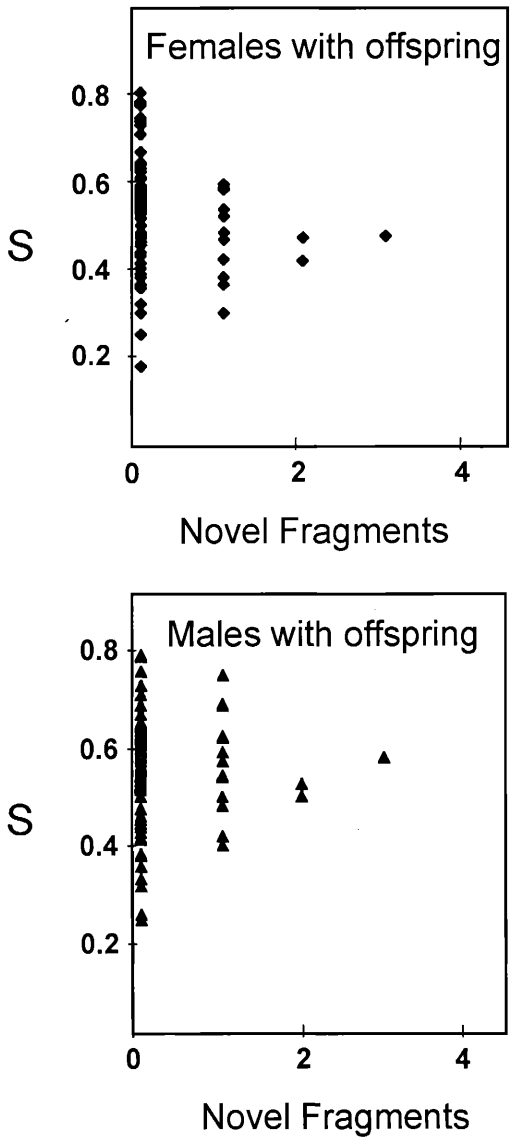

FIG. 2. Band-sharing among putative Carolina Wren parents and nestlings. Symbol location denotes the proportion of bands in a nestling's fingerprint shared with putative mother and father, and plotted against the number of bands in the nestling's fingerprint that were not in the putative parents fingerprint (novel fragments).

number of novel fragments shows that those individuals with 1, 2, or 3 novel fragments have high levels of band-sharing (Fig. 2), providing additional evidence that the 84 nestlings in 23 nests cannot be excluded from the adults attending those nests.

Discussion.—We found no evidence of a mixed reproductive strategy in our population of Carolina Wrens. The lack of ISBP was expected because we did not find any nests in which more than one egg had been laid over a 24 h period.

Factors that may affect opportunities for EPFs include breeding synchrony (Stutchbury and Neudorf 1998), population density (Westneat et al. 1990, Westneat and Sherman 1997, Møller and Ninni 1998), and mate guarding (Westneat et al. 1990, Currie et al. 1999). Westneat (1990) proposed that breeding synchrony should reduce frequency of EPP because males would be too busy guarding mates to engage in extrapair copulations (EPCs). Stutchbury and Morton (1995), however, proposed that breeding synchrony allows females to evaluate male quality and promotes EPP in some species. Our population had an overall low synchrony index value (i.e. 15.4% ± 11), which supports the Stutchbury and Morton (1995) hypothesis.

Although population densities during the years of this research were not the highest observed on the study site (i.e. 15 individuals/10 ha), territorial boundaries expand and are often shared even during low-density years (T. Haggerty pers. obs.). Therefore, we suspect that opportunities for EPFs existed and that a low density was not the primary cause for genetic monogamy in our population.

Although mate guarding may have occurred in our population, fledgling care should have limited the male's ability to guard their mates during the fertile periods of subsequent broods (Weatherhead and McRae 1990; but see Møller 1991, Conrad et al. 1998). Yet, we found no extrapair young in subsequent broods (i.e. 7 nests, 27 nestlings). Furthermore, territorial advertisement and defense in a visually occluded habitat should have made mate guarding difficult (Westneat et al. 1990) and some EPFs possible, yet none was recorded. Our population also has a low divorce rate (i.e. 2 of 36 cases from 27 pairs over 12 breeding seasons in which both pair members survived from one breeding season to the next), which is contrary to what is predicted when monogamy is enforced (Birkhead and Møller 1996, Gowaty 1996), but is expected when EPP rates are low (Cezilly and Nager 1995). Therefore, we doubt that mate guarding constrained females from engaging in extrapair activities.

As expected for a species with a low EPF rate (Birkhead and Møller 1996), males in our population contributed substantially to offspring care (Haggerty and Morton 1995, T. Haggerty unpubl. data). Although males do not incubate, they provide food to nestlings and females. In addition, nesting-interval data (Haggerty and Morton 1995) show that females lay and incubate new clutches well before fledglings from previous broods reach independence. Therefore, male care during the fledgling period may be essential if multiple broods are to be raised by a pair during a prolonged breeding season (Westneat et al. 1990). The threat of male desertion or reduced care

may constrain females from engaging in EPCs (Møller 1988, Burke et al. 1989, Dixon et al. 1994). Further, in sedentary species like the Carolina Wren, females may need mutually defended resources year round for their survival. Females engaging in EPCs may lose access to defended resources (Møller 1988, Westneat and Gray 1998). Most Carolina Wren mortality occurs during winter (Haggerty and Morton 1995, T. Haggerty unpubl. data) and females that have a mate may have a better chance of surviving and breeding another year than unfaithful and unmated females.

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Does Red-Cockaded Woodpecker Excavation of Resin Wells Increase Risk of Bark Beetle Infestation of Cavity Trees?

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The Red-cockaded Woodpecker (*Picoides borealis*) is unique among North American woodpeckers in that it nests and roosts nearly exclusively in living pines (*Pinus* spp.). Red-cockaded Woodpeckers make daily excavations at small wounds, termed "resin wells," around their cavity entrance and on the bole of their cavity tree, from which resin flows down the tree (Ligon 1970). The woodpeckers also flake off loose bark which results in a smoother surface on the pine tree's bole. Those behaviors result in a resin barrier that serves as an effective defense against rat snakes (*Elaphe* spp.; Jackson 1974, Rudolph et al. 1990). Rat snakes regularly attempt to climb active Red-cockaded Woodpecker cavity trees (cavity trees currently in use for nesting and roosting) and are known to prey on Red-cockaded Woodpeckers when the resin barrier is inadequate (Jackson 1978b, Neal et al. 1993). The resin barrier is believed to increase the probability of a breeding pair's nest success and survival of roosting woodpeckers (Conner et al. 1998).

Red-cockaded Woodpecker cavity trees in eastern Texas, especially active cavity trees, are regularly attacked and killed by southern pine beetles (*Dendroctonus frontalis*) and occasionally by various species of engraver beetles (*Ips* spp.; Conner et al. 1991, Conner and Rudolph 1995, Rudolph and Conner 1995). The pine tree's resin, which woodpeckers use to create a barrier against rat snakes, serves also as the pine tree's primary defense against bark beetle infestation (Wahlenberg 1946, Hodges et al. 1977, Conner et al. 1998). The resin's flow rate and total production (yield) influence the pine tree's ability to physically repel a bark beetle attack. However, daily maintenance of resin wells by woodpeckers may decrease the pine tree's resin yield, and thus, reduce its ability to repel attacks by bark beetles.

We examined resin yield and bark beetle infestation rates in Red-cockaded Woodpecker cavity trees in longleaf (*Pinus palustris*), loblolly (*P. taeda*), and shortleaf (*P. echinata*) pines. Longleaf pine is widely known to produce greater yields of resin than loblolly and shortleaf pines and, as a result, is much more resistant to bark-beetle infestation (Hodges et al. 1977). Thus, if Red-cockaded Woodpeckers affect the ability of cavity trees to produce resin, the effect would most likely occur in loblolly and shortleaf pines. Also, if woodpecker activity at resin wells does increase susceptibility to bark beetles, the increase in bark-beetle-induced mortality should be

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