problems in studies of avian nest defence. Anim. Behav. 34: 561–566.

- LEFFELAAR, D., & R. J. ROBERTSON. 1986. Equality of feeding roles and the maintenance of monogamy in tree swallows. Behav. Ecol. Sociobiol. 18: 199– 206.
- MARTINDALE, S. 1982. Nest defense and central place foraging: a model and experiment. Behav. Ecol. Sociobiol. 10: 85–89.
- MONTGOMERIE, R. D., & P. J. WEATHERHEAD. 1988. Risks and rewards of nest defence by parent birds. Q. Rev. Biol. 63: 167-187.
- NUR, N. 1988. The consequences of brood size for breeding Blue Tits: III. Measuring the cost of reproduction: survival, future fecundity, and differential dispersal. Evolution 42: 351–362.
- PAYNTER, R. A., JR. 1954. Interrelations between clutch-size, brood-size, prefledging survival, and weight in Kent Island Tree Swallows. Bird-Banding 25: 35-58, 102–110, 136–148.
- POWELL, G. V. N. 1974. Experimental analysis of the social value of flocking by starlings (Sturnus vul-

garis) in relation to predation and foraging. Anim. Behav. 22: 501–505.

- QUINNEY, T. E., D. J. T. HUSSELL, & C. D. ANKNEY. 1986. Sources of variation in growth of Tree Swallows. Auk 103: 389-400.
- RØSKAFT, E. 1985. The effect of enlarged brood size on the future reproductive potential of the rook. J. Anim. Ecol. 54: 255–260.
- SHIELDS, W. M. 1984. Barn Swallow mobbing: self defence, collateral kin defence, group defence, or parental care? Anim. Behav. 32: 132–148.
- WHEELWRIGHT, N. T., J. LEARY, & C. FITZGERALD. In press. The costs of reproduction in Tree Swallows (*Tachycineta bicolor*). Can. J. Zool.
- WIGGINS, D. A. 1990. Food availability, growth, and heritability of body size in nestling Tree Swallows (*Tachycineta bicolor*). Can. J. Zool. 68: 1292– 1296.
- WILLIAMS, J. B. 1988. Field metabolism of Tree Swallows during the breeding season. Auk 105: 706– 714.

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Habitat Occupancy by Bachman's Sparrow in the Francis Marion National Forest before and after Hurricane Hugo

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The effects of catastrophic environmental events on avian populations are of interest to population ecologists and conservation biologists. Models of population viability have pointed to environmental catastrophes as a major cause of extinction of small populations (Ewens et al. 1987). The specific effects of such events, however, are rarely documented in nature because comparable data collected before the catastrophe are rarely available.

On 21 September 1989, Hurricane Hugo slammed into coastal South Carolina and caused widespread destruction in the Francis Marion National Forest, Berkeley County, South Carolina. Loss of harvestable timber in some portions of the National Forest was estimated at 75% (LeGrand 1990). After the storm, the U.S. Forest Service cleared large areas of downed timber to lessen the danger of fire and bark beetle outbreaks. The impact of the storm and subsequent clearing of canopy trees on avian species associated with longleaf pine (*Pinus palustris*) forest was obvious and severe, especially for pine specialists such as the Redcockaded Woodpecker (*Picoides borealis*) (LeGrand 1990). The impacts on species that are less closely associated with canopy trees are less clear. We documented changes in habitat occupancy by Bachman's Sparrow (*Aimophila aestivalis*) in the Francis Marion National Forest before and after the hurricane. In this note we describe the changes in occupancy and discuss their potential causes.

Bachman's Sparrow is a resident of open mature pine forests and clear-cuts of the southeastern United States (Dunning and Watts 1990). These habitats share a combination of a dense ground layer of grasses and forbs, and an open understory. We counted Bachman's Sparrows in the summer of 1988 as part of a study of habitat occupancy in different regions of the South Carolina coastal plain (Dunning and Watts 1990). In the summer of 1990 we resurveyed most of our 1988 study plots to determine if patterns of habitat occupancy had changed since the hurricane. Because we used somewhat different techniques to record densities in the two years, our density estimates were not directly comparable. Therefore, we examined changes in site occupancy between years by comparing presence/absence data from the two studies.

Methods (1988 survey).—We surveyed 24 plots in the Witherbee District of the Francis Marion National Forest in May and June, 1988 (Dunning and Watts 1990). These plots consisted of young clear-cuts (1–5 yr since planting), young (6–15 yr) and middle-aged (16–68 yr) pine plantations, and mature pine stands (>80 yr old). We counted sparrow populations by conducting point counts at each of six marked reference points within each plot, and recorded all birds seen and heard within the plots for 3 min. After this initial count, we played tape-recorded Bachman's Sparrow songs for 1.5 min, and listened for sparrow response for an additional 1.5 min. Including travel time between reference points, each count took about 45 minutes. Each plot was surveyed twice.

Methods (1990 survey).—In June and July, 1990, 9 months after the hurricane, we resurveyed 17 of our original plots, including 6 clear-cuts, 1 middle-aged stand, and 10 mature pine stands. We concentrated our efforts on these stand age-classes because our initial work in 1990 revealed no sparrows in young stands and most middle-aged stands. In the following analysis, we lumped the middle-aged and mature categories into a single class of mature stands, because the single middle-aged stand we surveyed was structurally very similar to the mature stands. Plot sizes ranged from 9.3 to 23.0 ha (1988 mean [±SD]: 14.7 ± 4.21 ha; 1989 mean: 14.9 ± 4.06 ha).

We could not repeat our 1988 survey technique because most of our marked reference points (often large pines) were destroyed. In addition, the 1990 surveys were part of a broader survey of sparrow distribution, which necessitated a survey technique that required less time. We surveyed each plot by spending 20 min in each stand, playing tape-recorded songs every 1-2 min and listening for a response. We walked along the edges of each plot as well as into the interior of most stands in an effort to hear any resident male sparrow. Each plot was surveyed twice. Male Bachman's Sparrows respond to tape recordings of their song by counter-singing, often from exposed perches. Because each technique included the playing of tape-recorded song, and because male sparrows respond predictably to such recordings, we believe that the techniques used in each year effectively determined the presence of the species in each site.

When the initial 1990 surveys indicated that the sparrow use of the clear-cut and mature stands had changed since 1988, we added 9 additional study plots (5 clear-cuts, 4 mature stands) within the Witherbee District to increase sample sizes. In particular, we surveyed all of the clear-cut sites that we found in the portion of the Witherbee District in which we worked.

All study plots in the Witherbee District were heavily affected by the hurricane. Thus, we were unable to determine if changes in habitat occupancy by the sparrow were due to hurricane-associated changes or to between-year changes in the vegetation structure of the sites themselves. This is especially true for the clear-cuts, which change rapidly in the first years after planting. To evaluate this alternative, we added 16 study plots (10 mature stands, 6 clear-cuts) in the eastern portion of the National Forest (Wambaw District), which was not damaged extensively by the hurricane. As in the Witherbee District, we surveyed all clear-cut sites in the Wambaw District that we were able to locate.

In the 1988 surveys, Bachman's Sparrows were common in mature pine stands but rarer in clear-cuts. We recorded sparrows in 10 of 11 mature stands (91%), but in only 3 of the 6 clear-cuts (50%). Densities were also lower in the clear-cuts than in mature stands (clear-cuts: 0.08 birds/ha, n = 6; mature stands: 0.26 birds/ha, n = 10; t = 2.67, P < 0.02; Dunning and Watts 1990).

In 1990 sparrows were found with equal frequency in mature pine and clear-cut habitats in the Witherbee District. We found sparrows in 13 of 15 mature stands (87%) and 10 of 11 clear-cuts (91%). Of the original 1988 study plots, we found sparrows in 8 of 11 mature stands (73%) and 5 of 6 clear-cuts (83%). Densities in the two habitat types were not significantly different in 1990 (clear-cuts: 0.06 ± 0.03 , n = 6; mature stands: 0.09 ± 0.06 , n = 13; t = 1.50, P > 0.10).

We could have found sparrows in more clear-cuts in 1990 for at least two reasons. First, both the hurricane and the subsequent salvage operations changed the vegetation structure of the mature stands. In particular, logging equipment and operations destroyed much of the ground vegetation with which Bachman's Sparrows are closely associated (Dunning and Watts 1990). In mature stands that were not cleared, downed pines added considerable debris to the ground and understory layers (Dunning and Mays pers. observ.). Our previous work suggests that these changes should make the damaged stands less attractive to sparrows. It is possible that birds left the mature stands because of these changes and colonized nearby clearcuts, an alternative habitat that is readily used in other areas (Hardin and Probasco, 1983, Dunning and Watts 1990).

A second possibility is that the increased use of clear-cut habitat may have been due to an increase in the suitability of the clear-cuts themselves. Clear-cuts rapidly change their structural profile in the first years after pines are planted as the trees mature and grasses become better established. We have suggested that these changes strongly affect sparrow occupancy (Dunning and Watts 1990). To evaluate this possibility, we surveyed 16 sites in the undamaged Wambaw District. In this area we found sparrows in 6 of 10 mature stands, but no sparrows in any of 6 clear-cuts. The clear-cuts in the Wambaw District ranged from sites planted the previous year with little standing vegetation to older stands with more complex vegetative structure. Thus, we found no support in the undamaged portion of the study area for the hypothesis that site occupancy by the sparrow increased with age of the clear-cuts.

The high proportion of clear-cuts occupied by sparrows in the hurricane-damaged Witherbee District is similar to the pattern of occupancy in regions where mature pine stands are very rare (Dunning and Watts 1990). The pattern in the undamaged Wambaw District, where no sparrows were seen in clear-cuts, is similar to the habitat occupancy found in other South Carolina areas where mature pine is common (Dunning unpubl. data). Thus, one major effect that Hurricane Hugo may have had on the sparrow was to change the local pattern of habitat use. If mature pine and clear-cut habitats yield different levels of reproductive success or survivorship, such a change in habitat occupancy could have a long-term effect at the population level. The impact of large-scale catastrophes such as hurricanes has been documented recently for species whose habitat requirements are relatively well described (Engstrom and Evans 1990). We suggest that species, such as Bachman's Sparrow, whose habitat requirements are less understood should also be monitored to determine the ultimate effect of the hurricane on local avian populations.

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LITERATURE CITED

- DUNNING, J. B., & B. D. WATTS. 1990. Regional differences in habitat occupancy by Bachman's Sparrow. Auk 107: 463–472.
- ENGSTROM, R. T., & G. W. EVANS. 1990. Hurricane damage to Red-cockaded Woodpecker (*Picoides borealis*) cavity trees. Auk 107: 608-610.
- EWENS, W. J., P. J. BROCKWELL, J. M. GANT, & S. I. RESNICK. 1987. Minimum viable population size in the presence of catastrophes. Pp. 59-68 in Viable populations for conservation (M. E. Soule, Ed.). Cambridge Univ. Press, Cambridge.
- HARDIN, K. I., & G. E. PROBASCO. 1983. The habitat characteristics and life requirements of Bachman's Sparrow. Birding 15: 189–197.
- LEGRAND, H. E. 1990. The changing seasons—Fall 1989 report. Am. Birds 44: 252.

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A Deficient Diet Narrows Growth Bars on Induced Feathers

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The width of daily growth bars on feathers can be considered an index of the nutritional condition of birds at the time the feathers were grown (Grubb 1989). Removing a feather grown during normal molt causes regeneration of a replacement. This is an induced feather. The width of growth bars on the induced feather reflects the bird's nutritional condition during feather growth. Differences in daily growth bar width have been used as evidence that caching (Waite 1990) and supplementary food (Grubb and Cimprich 1990) improve the nutritional condition of free-ranging birds. Interpretation of these data, however, has been hindered by lack of experimental evidence that the width of growth bars on an induced feather is narrowed if a bird's diet is deficient during growth.

To demonstrate that feather growth and diet are related, I captured 15 male (wing cord \geq 62 mm)

Carolina Chickadees (Parus carolinensis) in Morrow County, Ohio, during the second week of January 1990. They were banded with USFWS bands and housed individually in 0.75-m³ welded-wire cages. The cages were arranged on individual 1-m-high tables in a 3 × 5 grid in a 3.7 × 5.2 × 2.2 m windowless room on the campus of Ohio State University. The top of each cage was left uncovered. The sides were wrapped in opaque white plastic sheeting, so the birds could hear but not see each other. Each cage had three 0.75-m long, 0.5-cm-diameter branches for perches, a cup for tap water, and separate food cups for shelled "gray-striped" sunflower seeds (Sunflower Natural Foods, Columbus, Ohio) and approximately 1.9-cm mealworms (Rainbow Mealworms, Compton, California). Water and the white plastic liner of the cage floor were changed daily. Room air temperature was 23°C and light: dark regime was 8:16 h. The six 150-W