

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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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 \times 5 grid in a 3.7 \times 5.2 \times 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

TABLE 1. Mean (\pm SD) widths of daily growth bars on induced (DGI) and original (DGO) feathers of Carolina Chickadees with access to 80, 90, or 100% of an *ad libitum* diet, and the induced/original ratios (DGI/DGO) of growth bar widths. So that *P* values from all Mann-Whitney *U* tests may be depicted clearly, results for the 80-percent treatment group are presented twice. Sample sizes are in parentheses.

Diet percent	DGI (mm)	<i>P</i> ^a	DGO (mm)	<i>P</i> ^a	DGI/DGO	<i>P</i> ^{b,c}
80	1.36 \pm 0.16 (5)	0.20	2.34 \pm 0.07 (5)	0.71	0.581 \pm 0.064 (5)	0.01 ^d
90	1.60 \pm 0.05 (4)		2.29 \pm 0.13 (4)			
100	1.55 \pm 0.19 (5)	0.21	2.23 \pm 0.13 (5)	0.14	0.733 \pm 0.062 (5)	0.27
80	1.36 \pm 0.16 (5)		2.34 \pm 0.07 (5)		0.581 \pm 0.064 (5)	0.006 ^d

^a Two-tailed Mann-Whitney *U* test.

^b One-tailed Mann-Whitney *U* test.

^c Test performed on arcsine-transformed values.

^d Significant at Bonferroni's procedure alpha level of 0.017.

incandescent lights came on at 1000 EST; a 5-W night-light was left on throughout each dark period.

To test the prediction that chickadees on deficient diets would grow an induced feather with narrower daily growth bars, I first determined the daily *ad libitum* consumption of both sunflower seeds and mealworms for each bird. Then, I reduced these amounts to 80% and 90% of *ad libitum* in two treatment groups. A control group was maintained on 100% of the *ad libitum* diet. When I provided each bird with *ad libitum* seeds and mealworms from 21 to 29 January, the birds adopted a feeding method that resulted in many partly eaten seeds and mealworms left on the cage floor. I could not measure daily food consumption by subtraction because an unknown amount of water evaporated from tissue in the discarded pieces of mealworm after the impermeable cuticle exoskeleton had been torn open. Therefore, from 30 January to 5 February, I determined for each of the 15 birds the exact *ad libitum* daily consumption of food that first coincided with an absence of spillage. On the first day of this period, I weighed known amounts of seeds and mealworms to the nearest 0.01 g on an Ohaus triple-beam balance, and I placed them in the two food cups of each bird's cage just before "lights on." Exactly 24 h later, I determined the aggregate masses of any seeds or mealworms that remained in the food cups. I also removed the plastic floor liner from each cage and hand-separated all pieces of seeds and mealworms from the previous day's accumulation of fecal material. For each of the two food types, I added the mass of spillage to the mass of food that remained in the food cup, and subtracted that sum from the amount provisioned the previous morning. I then reduced the upcoming day's allotments of seeds and mealworms by the amounts a bird had not consumed. By the end of 5 days I had determined for each bird the maximum provisions of seeds and mealworms that resulted in total removal of food from the food cups and no spillage. I considered these maximum no-spillage quantities to represent *ad libitum* consumption. All birds were then maintained on these *ad libitum* quantities for an additional week.

On 12 February, I employed a random numbers table to assign each chickadee to a treatment group, with the restriction that there be one bird from each of the three groups in each of the five "rows" of the grid. Before "lights on" on that day, I pulled the outermost right (R6) rectrix of each bird and provided the assigned percentage of its *ad libitum* consumption. Over the next 6 weeks, just before "lights on" each day, I gave each bird its assigned amounts of seeds and mealworms, a fresh supply of water, and a new plastic floor liner. On 3 April, I pulled the induced R6 rectrix and released the birds at the site of capture.

I measured the mean value of 10 daily growth bars on each feather (Grubb, 1989). To avoid introducing bias, I performed these measurements without knowing from which bird a feather had been taken. As an index of nutritional status, induced feather growth must be comparable across birds of different sizes. Therefore, I obtained a standardized index of feather growth (daily growth of induced rectrix divided by daily growth of original rectrix; DGI/DGO) by calculating the ratio of mean growth bar width on the induced feather (DGI) to mean growth bar width on the original feather (DGO; Grubb 1989). I determined the masses of induced and original feathers to the nearest 0.01 mg on a Mettler AE163 electronic balance, and I calculated a standardized index of mass (mass of induced rectrix divided by mass of original rectrix; MI/MO).

I used Mann-Whitney *U* tests to compare treatment groups (Siegel 1956). I employed Bonferroni's multiple comparisons procedure (DeVore and Peck 1986), which resulted in reduction of the alpha level to 0.017 for pairwise comparisons. All values reported in the tables are means and standard deviations of original data, proportions were arcsine-transformed before analysis. Tests of DGI/DGO ratios were considered to be one-tailed because the direction of the difference had been predicted; all other tests were treated as two-tailed.

One bird in the 90% treatment group died during the experiment, which reduced the sample size in this group to four. There were no significant pairwise

TABLE 2. Mean (\pm SD) masses of induced (MI) and original (MO) feathers of Carolina Chickadees with access to 80, 90, or 100% of an *ad libitum* diet, and the induced/original ratios (MI/MO) of masses. So that *P* values from all Mann-Whitney *U* tests may be depicted clearly, results for the 80-percent treatment group are presented twice.

Diet percent	MI (mg)	<i>P</i> ^a	MO (mg)	<i>P</i> ^a	MI/MO	<i>P</i> ^{a,b}
80	3.66 \pm 0.52 (5)		5.90 \pm 0.32 (5)		0.621 \pm 0.084 (5)	
90	4.55 \pm 0.46 (4)	0.04	6.03 \pm 0.66 (4)	0.90	0.756 \pm 0.028 (4)	0.017 ^c
100	4.06 \pm 0.48 (5)	0.33	5.54 \pm 0.11 (5)	0.39	0.744 \pm 0.100 (5)	0.90
80	3.66 \pm 0.52 (5)	0.35	5.90 \pm 0.32 (5)	0.17	0.621 \pm 0.084 (5)	0.12

^a Two-tailed Mann-Whitney *U* test.

^b Test performed on arcsine-transformed values.

^c Significant at Bonferroni's procedure alpha level of 0.017.

differences between treatment groups in the average width of growth bars on the induced and original R6 rectrix (Table 1). The DGI/DGO ratio was significantly smaller in the 80% group than in either the 90% or the 100% group. The latter two treatments did not differ statistically (Table 1). There were no significant pairwise differences in the mass of the induced and original R6 rectrix (Table 2). However, the MI/MO ratio was significantly greater in the 90% than in the 80% group (Table 2).

The results support the assumption that growth bar width is influenced by a bird's nutritional condition. While the effect of reduced food on feather growth was only minor in the 90% treatment group, the effect was clear in the 80% group (Tables 1 and 2). However, other factors apparently played a role in determining the daily rate of feather growth. Birds in the 100% treatment group were maintained on an *ad libitum* diet and in their thermoneutral zone (Munzinger 1974) where, by definition, the energy requirements of existence were at a minimum. Yet these birds grew an induced rectrix at a daily rate only 73% as great as the daily rate they had grown the original feather during the previous molting period. Besides present nutritional condition, daily feather growth in captivity is apparently responsive to other factors, some of which may vary circa-annually.

The MI/MO ratio varied significantly with percent of *ad libitum* diet (Table 2). This suggests that the total quantity of material incorporated into a feather is also responsive to a bird's nutritional condition. Free-ranging Gray Jays (*Perisoreus canadensis*) provided with extra food to cache in their year-round territories during the autumn regenerated a more massive induced R6 rectrix during the following winter than did controls (Waite 1990). A ratio of feather masses could be employed to monitor nutritional condition in systems where growth bars on induced feathers are difficult to discern.

I believe the use of feather growth bars to monitor nutritional condition (Grubb 1989) is strongly sup-

ported in its fundamental assumption. Other factors besides the short-term interplay of energy intake and expenditure, however, almost certainly influence feather growth rate. These experiments will be more accurately interpreted if treatment groups are matched in time (e.g. Grubb 1989, Waite 1990, Grubb and Cimprich 1990).

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