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FACTORS AFFECTING NUTRITIONAL CONDITION OF FLEDGLING FLORIDA SCRUB-JAYS: A PTILOCHRONOLOGY APPROACH[1]

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Abstract. Although predation and starvation are considered the prime causes of post-fledging mortality, uncertainty exists about the importance and timing of these two factors. Reproductive success in Florida Scrub-Jays (*Aphelocoma coerulescens*) is positively correlated with amount of oak scrub in a territory. Using ptilochronology, we assessed whether scrub-jay fledglings in different territories differed in nutritional condition, because differential nutritional condition could be responsible directly (starvation) or indirectly (depredation) for territory-specific mortality. We measured three indices of feather growth in young jays: feather total length was significantly positively related to proportion of a territory covered by open oak scrub, whereas the relationship between amount of oak scrub and feather mass or daily feather growth rate approached significance. These results suggest that nutritional condition plays a role in survival of young Florida Scrub-Jays and that relatively subtle differences in territory composition may contribute to variation in overall reproductive success.

Key words: Aphelocoma coerulescens, *fledgling survivorship, Florida Scrub-Jay, nutritional condition, open oak scrub, ptilochronology.*

Population regulation remains a central issue in avian ecology, with fledgling production and first-year survivorship currently considered the primary proximate variables controlling population size (Arcese and Smith 1988, Perrins 1991). An important component of mortality in first-year birds comes in the weeks between fledging and trophic independence. Although predation and starvation are considered the prime causes of such mortality, uncertainty exists about the importance and timing of these two factors during the post-fledging period. For example, Sullivan (1989) concluded that in Yellow-eyed Juncos (*Junco phaeonotus*), predation predominated during the days just after fledging, whereas starvation became important several weeks later during the first days after independence from the parents. By contrast, Woolfenden and Fitzpatrick (1990) and Mumme (1992) concluded that predation was the dominant cause of mortality in young Florida Scrub-Jays (*Aphelocoma coerulescens*) throughout the period between hatching and trophic independence. Although death by starvation is rare in all age classes of Florida Scrub-Jays (McGowan and Woolfenden 1990), a positive relationship exists between nestling size and fledgling survivorship (McGowan 1987, Fitzpatrick et al. 1988), suggesting that rate of food intake may indirectly affect predation-caused mortality. Well-fed nestlings and fledglings may beg less and remain motionless longer, thereby attracting fewer predators (Mumme 1992).

Florida Scrub-Jay populations are most dense in oak-shrub dominated, open scrubby flatwoods between 5 and 15 years post fire (Woolfenden and Fitzpatrick 1991, Breininger et al. 1995). Breininger et al. (1995) found that reproductive success was positively correlated with amount of oak scrub in the territory. If fledgling mortality is caused by predation and is relatively low in open oak scrub, then two complementary mechanisms might be responsible. First, independent of the nutritional condition of the fledglings, oak scrub may reduce predation either by making the young birds harder for predators to capture or, since the ground cover is sparse under oaks, by making predators easier for jays to detect (Breininger et al. 1995). Second, oak scrub might contain abundant food, permitting high feeding rates of nestlings and fledglings and therefore reducing the begging, thought to attract predators (Mumme 1992). If mortality is lower in open oak-dominated territories only because of lower predation, then nutritional condition should be independent of amount of oak scrub in the territory. If mortality is lower in open oak-dominated territories because either such territories contain more food or the better-fed fledglings there are less conspicuous, or both, then nutritional condition should be positively

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TABLE 1. Analysis of covariance ($n = 89$) for mean characteristics of the R6 rectrix of sibling Florida Scrub-Jay fledglings. Shown are F-values for both covariates and factors, followed by the slope in parentheses for covariates.

	Covariates				Factors		
	Day of year	Number of fledglings	Number of helpers	Mean tarsus length of parents (mm)	Year	Pairbond	Territory
Growth-bar width (mm)	0.54 (0.00)	1.36 (−0.04)	0.28 (0.02)	0.05 (0.08)	0.21	0.77	1.79*
Total length (mm)	0.75 (−0.03)	0.89 (−0.49)	2.35 (−0.75)	0.48 (0.83)	3.00*	5.11*	2.76***
Mass (mg)	1.87 (−0.04)	2.85 (−0.78)	2.22 (−0.64)	0.72 (1.10)	4.47*	4.57*	2.76***
df	1, 37	1, 37	1, 37	1, 37	4, 37	1, 37	43, 37

* $P < 0.05$, *** $P < 0.001$.

correlated with extent of oak cover. In order to test these two predictions, we employed ptilochronology (Grubb 1989, 1995) to index nutritional condition of fledgling Florida Scrub-Jays in territories differing in amount of open oak scrub. Ptilochronology rests on the assumption that the wider a feather's daily growth bars, the better the bird's nutritional condition while the feather was being grown. This assumption has experimental support (Grubb 1990, Grubb and Cimprich 1990), and ptilochronology has been used to index habitat quality in other systems (Grubb and Yosef 1994).

Our analysis addresses three questions: (1) is growth bar width a valid measure of nutritional condition in fledgling scrub-jays, (2) do factors other than territory quality cause variation in nutritional condition among fledglings in different territories, and (3) is nutritional condition of fledglings positively related either to amount of oak scrub or to its proportional representation in a territory?

METHODS

This report is part of a long-term demographic study of the cooperatively breeding Florida Scrub-Jay at the Archbold Biological Station, Lake Placid, Florida (Woolfenden and Fitzpatrick 1984, 1991, 1996). The on-going project routinely involves collecting data on size, post-fire successional stage, and vegetational composition of territories, number of helpers, breeding phenology, and body mass of nestlings and fledglings. Information on cover type and successional history was recorded using a geographic information system (ARC/INFO) at Archbold. We included in the present analysis all territories for which > 80% of the area had been mapped for cover type. Some territories meeting this criterion included small unmapped areas outside of the Archbold property that were unlikely to change the overall proportional vegetational composition of a territory.

In July 1990–1994, while measuring newly-independent young-of-the-year birds about 80 days after they fledged (Woolfenden 1978), Woolfenden plucked and stored the fully grown outermost right (R6) rectrix of each bird. This feather extends only 1–2 cm beyond the skin at the time a bird leaves the nest and growth to 12–14 cm is completed before trophic independence (Woolfenden 1978), therefore the feather's rate of growth in the interim can be taken as an index of fledgling nutrition. Using methods detailed elsewhere (Grubb 1989), Grubb calculated, in a "blind" fashion for each collected rectrix, the average width (mm) of 10 growth bars centered on a point two-thirds of the distance from the proximal end. Mass (mg) and total length (mm) of each feather also were determined in a blind fashion.

Brood sizes at time of plucking ranged from one to four ($\bar{x} \pm SD = 2.69 \pm 0.91$; $n = 113$). For all analyses, we averaged the feather measurements for all the young jays surviving in each territory each year. We considered such average values per territory to be the primary sampling units for the analysis. Alpha was set at 0.05. Except where stated otherwise, values presented are $\bar{x} \pm SE$.

RESULTS

Is growth bar width a valid measure of nutritional condition? We investigated this by regressing mean feather measurements on the mean body mass (bm) of the same brood when the nestlings were age 11 days posthatch ($n = 113$). The regressions were positive and significant for both growth bar width ($y = 2.87 + 0.01bm$; $P = 0.004$) and feather mass ($y = 40.75 + 0.15bm$; $P = 0.003$).

The regression for total feather length also was positive, but not significant ($y = 110.78 + 0.08bm$; $P = 0.104$). From these results, we concluded that at least growth bar width and total feather mass were valid indices of nutritional condition of the young jays postfledging.

Does any factor other than territory quality cause variation in nutritional condition among fledglings in different territories? We used analysis of covariance (Sokal and Rohlf 1981) to screen several potential causal factors (Table 1): day of year is the first day of incubation; number of fledglings is number of young that departed from the nest; number of helpers is all nonbreeding adult jays in the territory; mean tarsus length is the average for the breeding male and female in the territory; year varied from 1990 to 1994; the pairbond between the breeding male and female in the territory is classified as either new that year or continuing from one or more previous years; and territory is the identity of the territory, which remained constant over the five breeding seasons, thereby identifying the habitat patches occupied by different fledglings.

Of the variables tested, only territory was significantly related to growth bar width (Table 1). Year, pairbond, and territory were all significantly related to

TABLE 2. Analysis of covariance ($n = 98$) for mean characteristics of the R6 rectrix of sibling Florida Scrub-Jay fledglings in relation to their territories, year, and duration of the parents' pairbond. Shown are F-values for both covariates and factors, followed by the slope in parentheses for covariates.

	Covariates		Factors	
	Area of territory in open oak scrub (ha)	Proportion of territory in open oak scrub	Year	Pairbond
Growth-bar width (mm)	0.26 (−0.00)	2.88 (0.28)	1.12	0.64
Total length (mm)	2.71 (−0.15)	6.13 (6.64)*	0.11	3.43
Mass (mg)	0.32 (−0.04)	1.89 (3.03)	1.50	3.69
df	1, 91	1, 91	4, 91	1, 91

* $P < 0.05$.

both total length and mass of the rectrix. Rectrices of fledglings were longest (115.1 ± 1.0 mm; $n = 12$) in 1992 and shortest (114.4 ± 0.7 mm, $n = 28$) in 1991, whereas rectrices of fledglings in territories held by new pairs were shorter (113.8 ± 0.5 mm, $n = 54$) than those (115. 1± 0.5 mm, $n = 65$) of fledglings in territories where the pair had bred together at least once before. Rectrices grown in 1994 were heaviest (48.2 ± 0.7 mg, $n = 35$), whereas those produced in 1991 were lightest (47.1 ± 0.6 mg, $n = 12$). The young of new pairs produced lighter weight rectrices (47.2 ± 0.5 mg, $n = 54$) than did the young of continuing pairs (48.3 ± 0.4 mg, $n = 65$) (Table 1).

We next inquired whether differences in the amount of open oak scrub could be responsible for the significant variation among territories in nutritional condition of fledglings. We looked for relationships between feather characteristics and both the total area of oak in a territory and the proportion of a territory in oak cover. Because of the apparent differences in feather growth among years and with length of the parents' pairbond (Table 1), we also included year and pairbond in this second model.

No measure of feather growth was significantly related to either absolute area of open oak scrub or year (Table 2). However, the relationships of all three feather measures with proportion of oak cover were positive when the absolute area of open oak had been controlled statistically. The relationship between proportion of open oak scrub and total length of feather was significant ($P = 0.02$), whereas the relationship between proportion of open oak scrub and growth bar width or feather mass was not ($P = 0.09$ and 0.14, respectively). Both rectrix length ($P = 0.07$) and mass ($P = 0.06$) were nearly significantly related to the length of the parents' pairbond.

DISCUSSION

We found that the heavier a young jay was as an 11-day-old nestling, the better its feather growth during the post-fledging interval. Thus, because body mass reflects food intake rate, reason exists to consider feather growth, particularly growth bar width, to be a valid index of nutritional condition. The positive relationships between body mass on day 11 and measures of feather growth also suggest that differences in nutritional environment among territories during the nestling stage persisted into the fledgling stage.

For the jays we sampled, no change was evident in any of the three measures of feather growth with the day of the year that incubation began. Feather mass, but neither daily feather growth rate nor total length, approached a significant negative relationship with the number of fledglings in the territory. This result is difficult to interpret as it might be expected that daily feather growth and feather length, as well as feather mass, would be affected by the number of mouths to be fed in a territory during the period of trophic dependence. The lack of a correlation was not due to small variation in the independent variable because the standard deviation (0.91 fledglings per territory) was large compared to the mean (2.70 fledglings; $n = 113$).

According to our three measures of feather growth, the nutritional well-being of the dependent young seemed unrelated to the number of helpers in the territory. In a controlled experiment, Mumme (1992) showed that removing helpers reduced the survivorship of fledglings, but the mechanism of the reduction was unknown. The insignificant relationship that we found between number of helpers and nutritional condition of fledglings suggests that the reduction in fledgling survivorship in Mumme's study may have been caused principally by reduced group vigilance for predators in the absence of helpers, a conclusion also reached by McGowan and Woolfenden (1990).

No feather characteristic measured was related to the mean tarsus length of the parents, suggesting that any tendency for fledglings with structurally larger parents to grow their feathers any faster, longer, or heavier than fledglings with smaller parents was overwhelmed by the influence of other factors.

There was a trend, significant in Table 1 and nearly so in Table 2, for fledglings to grow longer, heavier feathers if their parents had bred together for more than one year. This result is consistent with recent findings that enduring pairs of Florida Scrub-Jays have higher reproductive success than first-time pairs (Marzluff et al. 1996).

Feather length varied significantly with proportion of territory in oak cover. Feather growth rate showed a similar trend, but the relationship was not significant (Table 2). These results lend some support to the idea that even within the relatively uniform Florida oak scrub, habitat composition of territories affects nutritional condition of fledgling jays. Moreover, growth rate as a young nestling is correlated with subsequent survival (McGowan and Woolfenden 1990), and our study showed that growth rate after fledging is correlated with nestling mass. Together, these results imply that nutritional condition of both nestlings and fledglings affects first year survival. As suggested by Mumme (1992), this effect could result from decreased predation rate owing to the quieter behavior of well-nourished fledglings. It could also result from accelerated achievement of the mobility required to escape from predators. In any case, our findings show that subtle differences in territory composition—specifically the proportional representation of oak scrub within the territory—may help determine overall reproductive success.

Competition for the highest quality territories is hypothesized as a pivotal force in the evolution of cooperative breeding (review in Koenig et al. 1992), but for most species it remains difficult to demonstrate exactly what constitutes a high quality territory. Florida Scrub-Jays strongly prefer to forage in open oak scrub (Woolfenden and Fitzpatrick 1984), and Breininger et al. (1995) showed that reproductive success varies with amount of oak cover in the territory. The present study complements Breininger et al.'s results by demonstrating proximate importance of territory configuration as well as overall habitat. Territories having higher proportions of oak cover conferred nutritional advantages over those with lower proportions, whereas total area of oak cover had virtually no nutritional effect (Table 2). We propose that territories containing a high proportion of oak cover permit more efficient foraging and reduce energetic cost of territorial patrolling compared to those with lower proportions of oak.

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LITERATURE CITED

ARCESE, P., AND J. N. M. SMITH. 1988. Effects of population density and supplemental food on reproduction in Song Sparrows. J. Anim. Ecol. 57:119–136.

BREININGER, D. R., V. L. LARSON, B. W. DUNCAN, R. B. SMITH, D. M. ODDY, AND M. F. GOODCHILD. 1995. Landscape patterns of Florida Scrub-Jay habitat use and demographic success. Conserv. Biol. 9:1442–1453.

FITZPATRICK, J. W., G. E. WOOLFENDEN, AND K. J. MCGOWAN. 1988. Sources of variance in lifetime fitness of Florida Scrub-Jays. Proc. Int. Ornithol. Congr. 19:876–891.

GRUBB, T. C., JR. 1989. Ptilochronology: feather growth bars as indicators of nutritional status. Auk 106:3314–320.

GRUBB, T. C., JR. 1990. A deficient diet narrows growth bars on induced feathers. Auk 108:725–727.

GRUBB, T. C., JR. 1995. Ptilochronology: review and prospectus. Current Ornithol. 12:89–114.

GRUBB, T. C., JR., AND D. A. CIMPRICH. 1990. Supplementary food improves the nutritional condition of wintering woodland birds: evidence from ptilochronology. Ornis Scand. 21:277–281.

GRUBB, T. C., JR., AND R. YOSEF. 1994. Habitat-specific nutritional condition in Loggerhead Shrikes (*Lanius ludovicianus*): evidence from ptilochronology. Auk 111:756–759.

KOENIG, W. D., F. A. PITELKA, W. J. CARMEN, R. L. MUMME, AND M. T. STANBACK. 1992. The evolution of delayed dispersal in cooperative breeders. Quart. Rev. Biol. 67:111–150.

MARZLUFF, J. M., G. E. WOOLFENDEN, J. W. FITZPATRICK, AND R. P. BALDA. 1996. Breeding partnerships of two New World jays, p. 138–161. *In* J. M. Black [ed.], Partnerships in birds. Oxford Univ. Press, Oxford.

MCGOWAN, K. J. 1987. Social development in young Florida Scrub-Jays (*Aphelocoma c. coerulescens*). Ph.D. diss., Univ. South Florida, Tampa, FL.

MCGOWAN, K. J., AND G. E. WOOLFENDEN. 1990. Contributions to fledgling feeding in the Florida Scrub-Jay. J. Anim. Ecol. 59:691–707.

MUMME, R. L. 1992. Do helpers increase reproductive success: an experimental analysis in the Florida Scrub-Jay. Behav. Ecol. Sociobiol. 31:319–328.

PERRINS, C. M. 1991. Constraints on the demographic parameters of bird populations, p. 190–206. *In* C. M. Perrins, J-D. Lebreton, and G. J. M. Hirons [eds.], Bird population studies: relevance to conservation and management. Oxford Univ. Press, Oxford.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. 2nd ed. W. H. Freeman, San Francisco.

SULLIVAN, K. A. 1989. Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaenotus*). J. Anim. Ecol. 58:275–286.

WOOLFENDEN, G. E. 1978. Growth and survival of young Florida Scrub-Jays. Wilson Bull. 90:1–18.

WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1984. The Florida Scrub-Jay. Princeton Univ. Press, Princeton, NJ.

WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1990. Florida Scrub-Jays: a synopsis after 18 years of study, p. 241–266. *In* P. B. Stacey, and W. D. Koenig [eds.], Cooperative breeding in birds. Cambridge Univ. Press, Cambridge.

WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1991. Florida Scrub-Jay ecology and conservation, p. 542–561. *In* C. M. Perrins, J-D. Lebreton, and G. J. M Hirons [eds.], Bird population studies: relevance to conservation and management. Oxford Univ. Press, Oxford.

WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1996. Florida Scrub-Jay (*Aphelocoma coerulescens*). *In* A. Poole and F. Gill [eds.], The birds of North America, No. 228. Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, DC.