

primarily as Na₂O. Wise (1944) listed concentrations of Na₂O ranging from 0.04 to 18.7% of the total ash. The ashes used by birds during my observations were from various tree species, and none of it was salty to my taste.

In feeder experiments Broom (1976) showed that hummingbirds consumed 0.27 M sucrose solutions and 0.27 M sucrose + 0.07 M NaCl solutions equally in preference to other concentrations but avoided more concentrated salt solutions. Carroll and Moore (1993) found strong preferences for feeders in which sugar solutions were supplemented with vitamins. Their system also contained high concentrations of calcium as an inadvertent component of the vitamin supplement. Bacon (1973) reported observing a single unidentified hummingbird apparently drinking ocean water from the surface of a quiet bay. The birds are evidently sensitive to and discriminate among the concentrations of a variety of dissolved substances in their diets.

Verbeek (1971) reported on hummingbirds eating sand grains, presumably for the calcium salts they contained. Furthermore, he suggested that this behavior was in response to the calcium deficit that accrued from egg production. A. S. Leopold (field notes; mentioned in Verbeek 1971) repeatedly observed one female or juvenile Allen's Hummingbird (*Selasphorus sasin*) apparently eating ashes from an outdoor fireplace. It may not be a coincidence that all of the birds we observed were nesting females.

The ash-eating birds we observed were probably utilizing a rich, convenient mineral source. Verbeek (1971) conjectured that the birds learn the locations

of calcium-rich soils by haphazard sampling of the environment. Since wood ashes are a readily identifiable source of essential minerals, I suggest that ash feeding by nesting birds may be more common than the limited records suggest.

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LITERATURE CITED

- BACON, P. R. 1973. Hummingbird drinking sea water. *Auk* 90:917.
- BEUCHAT, C. A., W. A. CALDER III, AND E. J. BRAUN. 1990. The integration of osmoregulation and energy balance in hummingbirds. *Physiol. Zool.* 63: 1059-1081.
- BROOM, D. M. 1976. Duration of feeding bouts and responses to salt solutions by hummingbirds at artificial feeders. *Condor* 78:135-137.
- CALDER, W. A., III, AND S. M. HIEBERT. 1983. Nectar feeding, diuresis, and electrolyte replacement of hummingbirds. *Physiol. Zool.* 56:325-334.
- CARROLL, S. P., AND L. MOORE. 1993. Hummingbirds take their vitamins. *Anim. Behav.* 46:817-820.
- VERBEEK, N. A. M. 1971. Hummingbirds feeding on sand. *Condor* 73:112-113.
- WISE, LOUIS E. 1944. Wood chemistry. Reinhold Publishing Corp., New York.

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Habitat-specific Nutritional Condition in Loggerhead Shrikes (*Lanius ludovicianus*): Evidence from Ptilochronology

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Over much of North America, the density of Loggerhead Shrikes (*Lanius ludovicianus*) has been steadily declining for much of the 20th century (see references in Yosef and Grubb 1992). Even populations formerly thought to be strongholds of the species (Droege and Sauer 1990) have recently been losing ground at 5 to 10% per year (Tyler 1992, Yosef 1992). Although sev-

eral causal factors for the decline have been implicated (e.g. H. M. Hands, R. D. Drobney, and M. R. Ryan unpubl. report), attention has recently focused on modern agricultural practices involving either habitat destruction or introduction of herbicides and insecticides (e.g. Anderson et al. 1978, Yosef and Grubb 1992). Despite considerable recent attention to the species, little is known about the possible effects of human-modified habitats on this shrike's survival and fecundity. Here, we report evidence that nutritional condition in Loggerhead Shrikes resident in south-

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central Florida may be habitat specific. Our results suggest that pastures and citrus groves, respectively, may be superior and marginal habitats for the species.

We assumed that the nutritional condition of shrikes could be assessed with the technique of ptilochronology (Grubb 1989). Recognizing that each growth bar on a feather represents 24 h of growth (Brodin 1993), this technique uses the width of growth bars as an index of a bird's nutritional condition at the time the feather was being grown. The wider the growth bars, the better the nutritional condition (see Grubb 1992). Substantial experimental evidence indicates that growth-bar width is a function of a bird's nutritional condition at the time the feather was being grown (Grubb and Cimprich 1990, Waite 1990, Grubb 1991, White et al. 1991). Although Murphy and King (1991) did not measure growth-bar width, they found that daily feather growth was reduced in White-crowned Sparrows (*Zonotrichia leucophrys*) maintained on deficient diets. Despite these findings from other passerines, no experimental evidence indicates that growth-bar width reflects dietary adequacy in Loggerhead Shrikes. For our study, therefore, we assumed that growth-bar width is a valid indicator of nutritional condition in this species. The assumptions and utility of ptilochronology have been discussed further in Murphy and King (1991), Grubb (1992), and Murphy (1992).

Methods.—During March and April of 1992 and 1993, we live-trapped shrikes along 524 km of roadway through Charlotte, DeSoto, Hardee, Highlands, Glades, and Okeechobee counties, Florida. The habitat in the vicinity of each capture site was recorded as: (1) built-up urban, (2) palmetto scrub, (3) citrus, or (4) fenced pasture. At every capture site, the habitat was the same on both sides of the road. Before releasing each bird at the capture site, we determined age and sex, recorded tarsus length, and pulled and stored the right fourth (R4) rectrix. Growth bars are most easily discerned on feathers that are not pied or marked by pigment bars. While previous studies have used the outermost (sixth) rectrix, in Loggerhead Shrikes the fourth rectrix is the outermost that is predominantly monochromatic.

For each feather we measured: (1) mean width of 10 growth bars centered on a point two-thirds the distance from the proximal end of the feather (Grubb 1989); (2) total length; and (3) mass. Feathers were coded by R.Y. so that T.C.G. could measure them in a "blind" fashion without knowing from which of the four habitat types they had been taken.

We restricted analysis to feathers from birds known to be adults (after-second-year [ASY] birds at time of capture). Shrikes in southern Florida appear to spend their entire adult lives on the same territory (Yosef 1992). Therefore, we assumed that the feathers we collected from adults had been grown at the same site during the prebasic molt of the previous autumn. However, as second-year (SY) birds could have grown

TABLE 1. *F*-statistics from general linear models for characteristics of R4 rectrix ($n = 64$) of Loggerhead Shrikes resident in south-central Florida.

Feather variable	Covariate Tarsus length	Factor		
		Year	Sex	Habitat
Growth-bar width (mm)	1.77	0.40	5.97*	5.90***
Total length (mm)	0.17	0.26	0.43	2.11
Mass (mg)	0.36	0.80	0.88	5.19**

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; others not statistically significant ($P > 0.05$).

their R4 rectrix in a different habitat before dispersing to the site where we caught them, we omitted their rectrices from the analysis.

Analyses used general linear-regression models (GLM; Cohen and Cohen 1983, Anonymous 1991). Following GLM procedure with qualitative variables, we used *t*-test comparisons of regression coefficients between each habitat group and the mean of all habitat groups (Neter et al. 1989). Such a procedure allowed us to avoid the loss of statistical power resulting from correcting for experimentwise error (Anonymous 1991). Using standard analysis of residuals, we determined that our data met the assumptions for using GLM models (Cohen and Cohen 1983, Neter et al. 1989). Statistical significance was accepted at the 0.05 probability level. Birds of different size could have grown feathers at different rates during the molt, resulting in differences among R4 rectrices unrelated to sex or habitat type. We controlled for bird size by entering tarsus length as a covariate in our models. Finally, we checked for variation between 1992 and 1993 by including year as a factor.

Results.—The total length of the R4 rectrix was not significantly related to tarsus length, year, sex, or habitat type (Table 1). Daily growth ($P = 0.001$) and total mass ($P = 0.003$) of the feather, however, were both significantly related to habitat type, but not to tarsus length or year. Daily growth, but not total mass, was significantly related to sex ($P = 0.018$). Feathers of birds in citrus groves differed significantly in both growth-bar width and mass from the mean values of all four habitat types (Table 2). The *t*-values and the adjusted means in Table 2 indicate that the rectrices of shrikes in citrus groves grew less each day and were less massive when fully grown than the average rectrix from all four habitats. By contrast, rectrices from shrikes in pastures were longer, were heavier, and had wider growth bars than the average for the four habitats (Table 2). Growth-bar width, total length, and total mass of rectrices from urban or scrub habitats were not statistically different from the mean values for all four habitats (Table 2).

TABLE 2. General-linear-model comparisons of each of four habitat types with mean of four habitat types for characteristics of R4 rectrix of Loggerhead Shrikes resident in south-central Florida. $\bar{x} \pm \text{SD}$, with *t*-value in parentheses.

Feather variable	Habitat type			
	Urban (<i>n</i> = 16)	Scrub (<i>n</i> = 10)	Citrus (<i>n</i> = 14)	Pasture (<i>n</i> = 24)
Growth-bar width (mm)	3.50 ± 0.05 (1.08)	3.45 ± 0.06 (0.07)	3.28 ± 0.05 (-3.66***)	3.56 ± 0.04 (2.52*)
Total length (mm)	98.54 ± 0.83 (0.03)	97.93 ± 1.04 (-0.69)	97.51 ± 0.86 (-1.37)	100.09 ± 0.68 (2.09*)
Mass (mg)	28.88 ± 0.52 (-0.36)	28.54 ± 0.66 (-0.94)	28.13 ± 0.54 (-1.99*)	30.64 ± 0.43 (3.47***)

*, *P* < 0.05; ***, *P* < 0.001; others not statistically significant (*P* > 0.05).

Discussion.—Taken together, our findings suggest that in each of two years something about pastures and citrus groves, respectively, improved and worsened nutritional condition in molting resident shrikes. However, at least one other explanation must be considered. The birds in pastures and citrus groves, respectively, could have been of high and low quality to begin with, perhaps having been imprinted on these habitats while raised there, or having taken up residence in the two habitats because of social status. Thus, the robust feather growth in pastures and the poor growth in citrus groves could have depended on the individual birds rather than the habitat. As evidence against this explanation, however, we note that shrikes in pastures or citrus groves were not unusual in size. For example, tarsus length was not related to habitat type ($F = 0.370$, $P = 0.774$).

Assuming that the rate of feather growth in pastures and citrus groves was affected by habitat type rather than bird quality, its causation could have been direct, indirect, or both. In central Florida, shrike populations are densest in pastures, which suggests that short grass and abundant fence-post hunting perches together provide superior foraging habitat and consequent excellent nutrition for the species (Yosef 1992).

In Florida, citrus is routinely sprayed during the autumn with miticide/insecticide compounds (T. Hurner pers. comm.) known to be toxic to nontarget organisms (Hayes and Laws 1991). Such chemicals could have had a chronic, sublethal effect on shrikes sufficient to retard feather growth. Alternatively, application of miticide/insecticides in the groves could have reduced the shrikes' food supply, thereby reducing the birds' nutritional condition sufficiently to be detectable using ptilochronology. Also, it seems possible that nutritional condition could have been lowered by direct and indirect effects of citrus-grove management practices. While it may be of interest to separate the two classes of causation experimentally, it seems clear that feeding rates (cf. Yosef and Grubb 1992), induced feather growth (Grubb 1989), survivorship, and fecundity of shrikes living in citrus groves should be examined.

Ptilochronology may be useful for evaluating the influence of various natural and disturbed habitats

on the nutritional condition of free-ranging birds. As revealed by our study, daily growth-bar width appears to be the most sensitive of the three indices investigated. Total feather length and feather mass could be less sensitive because their values change with feather wear through time, particularly in highly abrasive environments such as the sand ridges occupied by the shrikes we studied. By contrast, feather wear cannot affect the width of daily growth bars.

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LITERATURE CITED

- ANDERSON, W. L., AND R. E. DUZAN. 1978. DDE residues and eggshell thinning in Loggerhead Shrikes. *Wilson Bull.* 90:215-220.
- ANONYMOUS. 1991. Minitab reference manual. Release 8. Minitab, State College, Pennsylvania.
- BRODIN, A. 1993. Radio-ptilochronology: Tracing radioactively labelled food in feathers. *Ornis Scand.* 24:167-173.
- COHEN, J., AND P. COHEN. 1983. Applied multiple regression/correlation analysis for the behavioral sciences, 2nd ed. Lawrence Erlbaum Associates, Hillsdale, New Jersey.
- DROEGE, S., AND J. R. SAUER. 1990. North American breeding bird survey annual summary, 1989. U.S. Fish Wildl. Serv. Biol. Rep. 90.
- GRUBB, T. C., JR. 1989. Ptilochronology: Feather growth bars as indicators of nutritional status. *Auk* 106:314-320.
- GRUBB, T. C., JR. 1991. A deficient diet narrows growth bars on induced feathers. *Auk* 108:725-727.
- GRUBB, T. C., JR. 1992. Ptilochronology: A consideration of some empirical results and "assumptions." *Auk* 109:673-676.
- GRUBB, T. C., JR., AND D. A. CIMPRICH. 1990. Supplementary food improves the nutritional con-

- dition of wintering woodland birds: Evidence from ptilochronology. *Ornis Scand.* 21:277-281.
- HAYES, W. J., JR., AND E. R. LAWS, JR. (Eds.). 1991. Handbook of pesticide toxicology. Vol. 3, Classes of pesticides. New York, Academic Press.
- MURPHY, M. E. 1992. Ptilochronology: Accuracy and reliability of the technique. *Auk* 109:676-680.
- MURPHY, M. E., AND J. R. KING. 1991. Ptilochronology: A critical evaluation of assumptions and utility. *Auk* 108:695-704.
- NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1989. Applied linear regression models, 2nd ed. Irwin, Homewood, Illinois.
- TYLER, J. D. 1992. Nesting ecology of the Loggerhead Shrike in southwestern Oklahoma. *Wilson Bull.* 104:95-104.
- WAITE, T. A. 1990. Effects of caching supplemental food on induced feather regeneration in wintering Gray Jays *Perisoreus canadensis*: A ptilochronology study. *Ornis Scand.* 21:122-128.
- WHITE, D. W., E. D. KENNEDY, AND P. C. STOUFFER. 1991. Feather regrowth in female European Starlings rearing broods of different sizes. *Auk* 108:889-895.
- YOSEF, R. 1992. Territoriality, nutritional condition and conservation in Loggerhead Shrikes (*Lanius ludovicianus*). Ph.D. dissertation, Ohio State Univ., Columbus.
- YOSEF, R., AND T. C. GRUBB, JR. 1992. Territory size influences nutritional condition in non-breeding Loggerhead Shrikes: A ptilochronology approach. *Conserv. Biol.* 6:447-449.

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Influence of Abiotic Factors on Preroosting Behavior of Greylag Geese (*Anser anser*)

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In socially living birds like Greylag Geese (*Anser anser*), one of the most impressive behavioral propensities of the individual is its effort to keep in contact with the group (Lorenz 1988), that is, keeping track of its partner, family, and flock. This is particularly obvious in the evening, before birds fly to their roosts. In many birds roosting time is strongly influenced by abiotic factors (Eiserer 1984) and follows the rules of endogenous, light-entrained rhythmicity (Gwinner 1975).

Social interactions also have been shown to have entraining (review with bird examples by Mrosovsky et al. 1989) and disruptive effects (Regal and Conolly 1980) on circadian-rhythmic activity. This also may be the case in the timing of the departure to the roost. However, the delaying of the take-off because of social activity could be disadvantageous (e.g. starting or landing late at low visibility may lead to crashes; pers. obs., Schmitt 1991). Thus, one may predict that time of departure should not be affected by social interactions leading to group cohesion (synchronization and coordination caused by head shaking or tossing, vocalizations and adjusting movements; Rav-

eling 1969, Black and Barrow 1985, Black 1988, Lorenz 1988, Schmitt 1988, 1991).

Data necessary to quantify the association between group cohesion and departure time are difficult to collect in wild populations because both abiotic factors and group structure vary daily (e.g. number and identity of individuals). This problem did not exist in the tame flock of Greylag Geese I studied, the very same individuals living together for months at a time. Moreover, the social structure of the flock was stable and known during the summer. Actually, during each of both summers of my study, only three wild immigrants lived for some weeks within the flock and, altogether, only six adult individuals disappeared. Thus, this unique field situation provided an opportunity to determine if abiotic factors influenced both flock synchronization (which was used as a measure of group cohesion) and departure time to the roost, and/or if flock synchronization affected departure time.

Materials and methods.—I observed preroosting behavior in a free-living, but tame flock of about 150 Greylag Geese (mixed population of *Anser anser anser* and *A. a. rubirostris*) in Grünau/Almtal, Austria (47°48'N, 13°57'E) during two summers (22 July to 7 October 1986; 25 July to 11 September 1987). During daily moves between feeding and sleeping areas, the distances covered by the flock roughly corresponded

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