

Territory Size Influences Nutritional Condition in Nonbreeding Loggerhead Shrikes (*Lanius ludovicianus*): A Ptilochronology Approach

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Once relatively common throughout much of North America, the Loggerhead Shrike (*Lanius ludovicianus*) has recently undergone a precipitous decline and is currently diminishing in numbers at about 5% per annum (Graber et al. 1973; Morrison 1981; Bystrak 1983; Hands et al. 1989). Here, we use ptilochronology (Grubb 1989) to show that a reduced number of hunting perches is correlated with reduced nutritional condition in shrikes, which could be contributing to the population loss. Ptilochronology is a recently developed method for monitoring the nutritional condition of a free-ranging bird by measuring the width of daily growth bars on a tail feather induced to grow by pulling out its predecessor (Grubb 1989). That growth-bar width is related to nutritional condition is now clear (Grubb 1989, 1991; Grubb & Cimprich 1990).

A number of factors have been implicated in the Loggerhead Shrike's decline (Busbee 1977; Anderson & Duzan 1978; Craig 1978; Porter et al. 1978; Kridelbaugh

1982; Bystrak 1983; Cadman 1985; Hands et al. 1989). In the last decade of the twentieth century, however, loss of foraging habitat and hunting perches to modern agricultural practices seems the most likely explanation (Cadman 1985; Hands et al. 1989). This report focuses on hunting perches as a limiting resource in a habitat where foraging substrate and nest sites are unlikely to be limiting.

Shrikes do not hunt on the wing. Therefore, we hypothesized that a territorial shrike requires some minimum amount of grassland or pasture substrate within scanning distance from hunting perches, a portion of the territory we termed the "utilizable area." Recognizing that the density of hunting perches is variable, we also hypothesized that in areas with few hunting perches, a shrike must defend a very large area, and that populations have been declining because continual removal of fence rows and other hunting perches has made utilizable areas too costly to defend due to the increased dead space. Specifically, with the continual removal of hunting perches, the benefit-cost ratio of defending a territory eventually declines below some minimum threshold value as the ratio of utilizable area to dead

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space decreases. Once the benefit-cost ratio declines below the threshold value, the territory is abandoned.

We tested four predictions deduced from the hunting-perch hypothesis: (1) all territories comprising a local mosaic contain the same amount of utilizable area, (2) larger territories contain more dead space, (3) the benefit-cost ratio varies inversely with territory size, and (4) a shrike's nutritional condition, as indexed by rate of feather regeneration, varies inversely with territory size.

In general, because of the importance of the plumage coat for protection, thermoregulation, and locomotion, feather regeneration should proceed as rapidly as possible subject to constraints such as net energy intake. Reduction of feather growth might be considered a "compensatory mechanism" counterbalancing such constraints. Thus, the reduced growth of an induced feather might indicate a reduction in nutritional condition too minor to cause the net catabolism of body tissues and resulting mass loss that have been considered the definitive indicators of "nutritional stress" (King & Murphy 1985).

We studied postbreeding shrikes during June–August 1990 at the MacArthur Agro-ecology Research Center, Archbold Biological Station, Lake Placid, Florida, a 4000-ha working cattle ranch. Territorial shrikes were captured in baited noose traps and were banded for individual recognition with USFWS aluminum bands and color bands. We used the shrikes' aggressive responses to playbacks and taxidermic mounts to map the borders of all territories on the ranch. Territory size was calculated as the minimum polygon bounded by defended points of the habitat. During June, we pulled the R4 rectrix (tail feather) from territorial adult shrikes, allowed the induced rectrix to be regenerated, then recaptured the birds 5–6 weeks later, pulled the fully grown induced rectrix, and calculated the feather's daily growth. If larger shrikes secure smaller territories, faster daily feather growth in birds on small territories could be due simply to body size, independent of nutritional condition. Therefore, we checked for a relationship between territory size and body size. Unfortunately, we lack information on possible variation in prey density among territories. However, the grassland foraging habitat was quite uniform and the shrikes appeared to be taking similar types of prey, principally grasshoppers (Orthoptera) and dragonflies (Odonata).

Using a balanced sampling design, we determined activity budgets for all birds based on the following mutually exclusive categories: LOOKOUT, scanning from an exposed perch; PREEN, maintaining the condition of the plumage; REST, remaining out of sight in a bush or tree; HANDLE, capturing, eating, or caching prey; CHANGE, flying between lookout perches; CHASE, flying to pursue territory intruders. Benefit-cost ratios were calculated as prey captures per hour divided by

percentage of activity in flight (CHANGE + CHASE). To reduce the likelihood of pseudoreplication (Hurlbert 1984), we performed all analyses on a per-territory basis by averaging values for the male-female pair defending a common territory. For analysis, we employed simple regression and we angular-transformed percentages (Steel & Torrie 1960).

During the study period, we mapped 21 postbreeding territories, the fledglings having departed previously. Territory area varied by two orders of magnitude, from 0.17 to 14.59 ha. The two major categories of hunting perch were fence lines and cabbage palms (*Sabal palmetto*). On average over the 21 territories, shrikes flew from a perch down to the ground to catch prey a maximum of 6.5 m from fence lines and 9.2 m from palm trees. Combining this information with tabulations of fence-line length and number of palm trees, we calculated the amount of utilizable area for each territory ($\bar{x} = 7709 \text{ m}^2$; C.V. = 37.1%; $n = 21$). In support of prediction 1, the amount of utilizable area was unrelated to territory size ($r^2 = 0.08$; $P = 0.47$). We subtracted utilizable area from total area to determine the amount of dead space in each territory. In support of prediction 2, larger territories contained more dead space ($r^2 = 0.85$; $P < 0.001$).

As territory size increased, shrikes spent significantly larger proportions of their activity changing perches, chasing intruders, and capturing, eating, or caching prey (Table 1). While prey captures per hour, the benefit index, was not related to territory size, percentage of time in flight (CHANGE + CHASE), the index of cost, increased significantly on larger territories (Table 1). The benefit-cost ratio and the feather-growth index of nutritional condition were both significantly negatively related to territory size (Table 1; Fig. 1) and significantly positively related to each other ($r^2 = 0.55$; $P = 0.001$; Fig. 1). These results support predictions 3 and 4. Finally, there was no significant relationship between ter-

Table 1. Activity budgets, prey captures and daily feather growth of territorial post-breeding Loggerhead Shrikes, and their relationship with territory size. All N's = 21.

Component	\bar{x}	C.V. (%)	Regression on territory area		
			b	r^2	P
Lookout (%)	78.4	17	-0.68	0.08	0.20
Preen (%)	6.3	112	-0.76	0.14	0.10
Rest (%)	3.0	258	-0.22	0.01	0.70
Handle (%)	6.2	38	0.43	0.35	0.004
Change (%)	4.7	122	1.46	0.73	<0.001
Chase (%)	1.4	126	0.44	0.33	0.006
Change + chase (%)	6.1	112	1.52	0.79	<0.001
Prey captures hr^{-1}	7.4	8	-0.03	0.04	0.38
Benefit:cost ^a	2.6	72	-0.41	0.77	<0.001
Daily feather growth (mm)	2.00	26	-0.10	0.58	<0.001

^a (Prey captures hr^{-1}) (change + chase)⁻¹

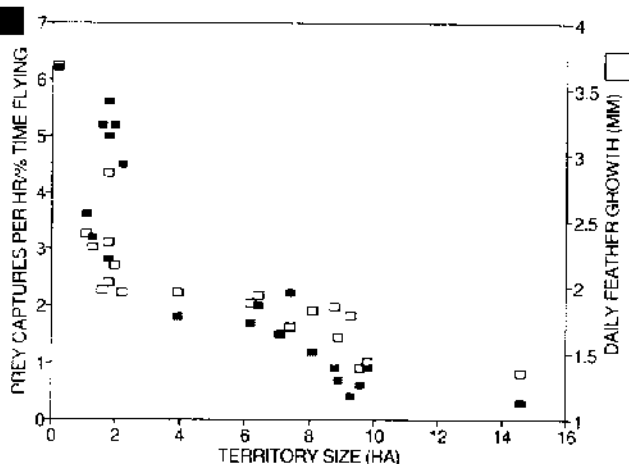


Figure 1. Relationships among a benefit-cost index of net energy intake (filled squares), an index of nutritional condition (empty squares) and territory size in postbreeding Loggerhead Shrikes.

territory size and body mass ($r^2 = 0.73$; $P = 0.48$). Thus, the negative relationship between feather growth and territory size was not confounded by body size.

Among the results in Table 1, the significant positive relationship between handling time and territory size is difficult to interpret. Because of our data-gathering approach, we cannot dissect HANDLE into its component parts. Thus, for example, we cannot investigate whether shrikes on small territories cached a larger number of prey, an activity that required less time than tearing apart and ingesting a freshly caught item. In any case, the trend in HANDLE was the same as the trends for CHANGE and CHASE. Furthermore, increases in all three of these activities were apparently compensated for principally by reductions in time spent in LOOKOUT and PREEN, though changes in these two categories only approached statistical significance.

These results support the hypothesis that density of hunting perches affects nutritional condition of non-breeding territorial shrikes. Areas of the ranch devoid of shrike territories were marked by few fences and sparse trees. Thus, these areas may have been subthreshold economically because of insufficient utilizable area. Similarly, the continuing decline of the Loggerhead Shrike may be at least partially due to withdrawal from parts of the species' range in which man's activities have reduced the density of hunting perches. Finally, this study illustrates the potential of daily feather growth as a convenient "biomarker" for assessing environmental quality.

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