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Resource Dependence and Territory Size in Loggerhead Shrikes (*Lanius ludovicianus*)

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Population declines of Loggerhead Shrikes (*Lanius ludovicianus*) have not been strongly correlated with the loss of preferred habitat (Bohall-Wood 1987, Brooks and Temple 1990). These findings suggest that factors other than breeding habitat are at least partially responsible and although, from time to time, researchers have searched for these other factors, no remedies for the situation have been found. U.S. Fish and Wildlife Service Breeding Bird Surveys (1966–1989) demonstrate that the Loggerhead Shrike is declining at a rate of about 5% per year continentwide. Of the 43 states censused during this period, shrike populations declined in 37 (86%; Robbins et al. 1986, Droege and Sauer 1990, Peterjohn and Sauer 1993). Although peninsular Florida, Oklahoma and New Mexico have been thought to be strongholds, Tyler (1992) and Yosef et al. (1993) have demonstrated that in both Oklahoma and peninsular Florida the species is declining at 5 to 9% per year.

A number of factors have been implicated in the Loggerhead Shrike's decline (Busbee 1977, Anderson and Duzan 1978, Bystrak 1983, Lymn and Temple 1991). However, in the last decade of the 20th century, the continuing loss of foraging habitat and hunting perches to modern agricultural practices seems the most likely explanation (Novak 1989, Pittaway 1991).

Shrikes are primarily sit-and-wait predators that hunt from conspicuous perch sites (Bohall-Wood 1987), and hunt on the wing only during adverse conditions (e.g. seasonal growth of annuals; Yosef and Grubb 1993), or when substantial numbers of prey are flying and can be caught easily.

Loggerhead Shrike territories must include suitable hunting perches and a nest site. Although trees and bushes may be important for other activities (e.g. hiding from predators, roosting), their importance as hunting perches has been demonstrated in Northern Shrikes (*L. excubitor*) by Askham (1990) and Yosef (1993), and in Loggerhead Shrikes by Yosef and Grubb (1992). In the latter study, areas with sparse trees and fence posts were devoid of shrike territories. Furthermore, with the use of ptilochronology (Grubb 1989), Yosef and Grubb (1992) illustrated that territory size influenced the nutritional condition of the defending bird. Shrikes defending smaller territories were in better condition.

The strategy of hunting from perches has limitations. The area scanned for prey can be considered as a concentric circle centered on a perch (Mills 1979), the radius of which is a function of perch height (Rice 1983, Sonnerud 1992), vegetation height, and density (Mills 1979, Yosef and Grubb 1993).

Because hunting perches are an important determinant of shrike territory size and configuration (Yosef 1993, Yosef and Grubb 1992), we hypothesized that Loggerhead Shrike population sizes could be enhanced by adding perches to reduce the total area defended by any given pair. Reduction in territory size would result from defending individuals using formerly unused areas within their territories that had not been used due to a lack of appropriate hunting perches. By reducing the size of existing territories, such a manipulation would allow additional pairs to set up breeding territories. We report on an experiment in which shrikes were offered additional hunting perches in a habitat where suitable foraging substrate and nest sites were unlikely to have been population-limiting factors.

Study area and methods.—We studied 22 territorial Loggerhead Shrike pairs at the MacArthur Agro-ecology Research Center (MAERC) of the Archbold Biological Station in Highlands County, southcentral Florida. MAERC is nearly equidistant from the Atlantic and Gulf of Mexico coasts of Florida, and is a 4,200-ha working cattle ranch that has extensive bahia-grass pastures, cabbage palm (*Sabal palmetto*) hammocks, native wetlands, and live oak (*Quercus virginiana*) uplands.

Birds were captured in baited traps and banded for individual recognition with U.S. Fish and Wildlife Service aluminum bands and color bands. We used the shrikes' aggressive responses to playbacks and taxidermy 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. All territories were mapped before (July–August 1991) and after (January–February 1992) the hunting perches were selectively added.

For the manipulation, we arranged 22 territories into 11 matched pairs of territories based on similar size, proportion of area useable for hunting, and prevalence of existing hunting perches (Table 1). One of each pair of territories was randomly assigned to either the control or manipulated group.

In August and September 1991, we introduced round, wooden fence posts (average height above

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TABLE 1. Characteristics of 11 matched pairs of territories, and extent of manipulation. "C" denotes control territories and "M" manipulated territories.

Matched pair	Perches added to M	Territory before (ha)		Usable area for hunting (ha)		Territory after (ha)		Difference (ha)	
		C	M	C	M	C	M	C	M
1	8	4.7	5.3	0.70	0.86	4.8	1.5	0.1	-3.8
2	8	5.1	8.0	0.73	0.80	5.2	1.3	0.1	-6.7
3	8	6.4	8.0	0.96	0.89	6.1	2.0	-0.3	-6.0
4	9	8.1	8.6	1.10	1.24	8.5	2.7	0.4	-5.9
5	9	8.3	9.3	1.03	0.95	8.4	1.5	0.1	-7.8
6 ^a	9	8.9	9.3	0.80	0.84	9.0	1.6	0.1	-7.7
7	7	8.9	9.6	0.87	0.70	9.1	2.6	0.2	-7.0
8	8	10.3	11.0	0.87	0.81	10.1	3.0	-0.2	-8.0
9	8	12.3	11.1	0.98	0.74	11.9	2.3	-0.4	-8.8
10	8	14.9	13.6	0.81	1.12	14.5	4.0	-0.4	-9.6
11	8	17.5	17.5	0.87	0.97	17.1	3.3	-0.4	-14.2

^a This pair of territories deleted from analysis of life-history characteristics because female in control territory disappeared early in breeding season.

ground $135 \pm \text{SD of } 6.3 \text{ cm}$, $n = 100$) into manipulated territories. Posts were introduced into areas of such territories not previously used for hunting as shown by lack of pounces and captures. Barbed wire was nailed to the top of each post in order to improve its usefulness as a hunting, feeding and caching site for the shrikes. Once a week we evaluated all posts for "perch use." Intensity of perch use was assessed using an index of fecal accumulation on posts. Because other bird species were also observed to use the posts, we also searched for shrike regurgitation pellets within a 0.5-m radius of each perch site. Both before and after the manipulation, all territories were mapped on aerial photographs (1 cm = 49 m [1 in = 400 ft]) and digitized with ArcInfo software.

In addition to comparing the areas defended by control and manipulated shrikes during the 1992 breeding season (February-June), we evaluated such life-history traits as number of nesting attempts, Julian day the first egg was laid, clutch size, egg-mass loss, hatching success, body mass and tarsus length of nestlings on day 10 after hatching, food-delivery rate to the nest, fledging success, number of young fledged per pair for the whole season, and blood-parasite load of young on day 13 posthatching.

Nesting frequency included all nest attempts made by a pair during the season, and included first, replacement, second, and third broods. We calculated egg-mass loss (ΔM) as

$$\Delta M = (M_i - M_{H_i})/M_i, \quad (1)$$

where M_i is the initial mass (to the nearest 0.1 g) and M_{H_i} is the mass prior to hatching. We considered hatching success to be the percent of eggs that produced nestlings by the day after the first egg hatched. Nestling body mass (to nearest 0.1 g) and tarsus length (to nearest 0.1 mm) were measured on day 10 posthatching in order to minimize the possibility of young leaving the nest prematurely due to handling (Lohrer 1974). Food-delivery rate was established by three

observers (using $10\times$ binoculars or $25\times$ telescope). Each nest was observed from a distance of 25 m for 2 h per day, between 0700 and 0900 EST, when young were 7, 10, and 13 days old. Previous studies have established that maximum feeding rates of shrike parents occur between 0600 and 1100 and when nestlings are 6 to 12 days of age (Yosef 1989, Gawlik and Bildstein 1990). Each visit by a parent with prey in its beak was considered as food delivery irrespective of size or type of prey. We calculated fledging success as the percentage of eggs that resulted in fledglings.

We reasoned that young shrikes from larger territories with nutritionally deficient parents (Yosef and Grubb 1992) would be more susceptible to parasitic infection. Blood-parasite load in affected nestlings may affect their survival and, therefore, the reproductive success of the parents. To assess whether the manipulation was related to blood parasite load in young, we took blood smears from 15 and 14 nestlings, respectively, in manipulated and control territories. Smears were made with a drop of blood taken from the brachial vein. Blood slides were air dried, fixed in 100% methanol, stained with Giemsa's stain (Bennett et al. 1991), and examined for hematozoa (*Haemoproteus*, *Plasmodium*, *Leucocytozoon*, *Microfilaria*, *Trypanosoma*). On each smear approximately 100,000 red blood corpuscles (RBCs) were examined under oil immersion ($\times 100$). We used matched-paired t -tests for comparison of parameters between manipulated and control territories after arcsine transformation of percentage data. All data are presented as $\bar{x} \pm \text{SD}$, unless otherwise specified.

Results.—No significant difference existed between territory size of control (9.3 ± 3.8 ha) and manipulated groups (10.1 ± 3.2 ha) prior to the experiment (paired t -test = 1.1, 10 df, $P = 0.279$). However, after introduction of additional perches, the 11 manipulated territories (2.3 ± 0.9 ha) differed significantly in size; (paired t -test = 9.8, 10 df, $P = 0.0001$) from the controls. The manipulated pairs constricted their

TABLE 2. Life-history traits of manipulated and control groups of Loggerhead Shrikes in southcentral Florida ($\bar{x} \pm SD$). Each group consisted of 10 pairs (n if different from 10).

Parameter	Nests		<i>t</i> -value
	Control	Manipulated	
Nesting frequency	2.4 \pm 0.8	2.2 \pm 0.4	1.0
Julian day first egg laid	92.0 \pm 9.2	91.0 \pm 20.0	0.1
Clutch size (eggs)	3.8 \pm 0.9	3.5 \pm 0.8	1.0
Percent hatching success	33.8 \pm 47.6	35.0 \pm 45.5	0.5
Percent fledging success	24.4 \pm 37.9	38.0 \pm 48.1	-2.2*
No. fledglings/territory	1.8 \pm 2.4	3.1 \pm 2.9	-2.4*
Percent clutch mass loss	15.0 \pm 0.9 (8)	14.8 \pm 0.7 (6)	-1.0
Nestling body mass (g)	33.0 \pm 2.6 (18)	33.3 \pm 3.2 (31)	-0.2
Nestling tarsus length (mm)	26.0 \pm 1.1 (18)	26.3 \pm 1.1 (31)	0.5
Parental feeding rate (no. feeds/h)			
Day 7	14.4 \pm 1.9	13.8 \pm 1.2	-0.3
Day 10	13.8 \pm 1.4	13.8 \pm 1.0	0.0
Day 13	15.1 \pm 1.5	14.4 \pm 1.4	-0.6

*. $P < 0.05$.

territories an average of 76.6% (range 69 to 84%). However, no significant change occurred in the average area of control territories over the duration of the study (paired *t*-test = 0.7, 10 df, $P = 0.474$; Table 1). Six new territorial pairs settled in vacated areas along fence lines during the study period. The first two pairs were initially observed in mid-September, another pair arrived in November, and three more pairs established territories just before the breeding season began in February.

For comparison of life-history traits, we used the records from matched pairs of territories in which all adults were present throughout the breeding season. Because one female from a manipulated territory disappeared early in the season, these analyses of reproductive success were based on 10 matched pairs rather than the original 11 pairs of territories. No significant differences between manipulated and control territories occurred in nesting frequency, date the first egg was laid, clutch size, egg-mass loss, hatching success, nestling body mass or tarsus length at 10 days of age, number of young fledged, or parental food delivery rate (Table 2). However, statistically significant differences were found in fledging success and the number of fledglings per territory.

The 10 control pairs initiated nests between 17 March and 15 April, laid 24 clutches, and fledged 18 young from 6 clutches (i.e. 1.8 young per pair, or 1.1 young per nesting attempt). However, only four (40%) of the pairs fledged young. Sixteen of the remaining 18 nests were predated, and 2 were lost to inclement weather. Clutch-mass loss during incubation for the six clutches ranged from 14 to 16% of initial mass. The body mass of the 18 young on day 10 ranged from 28.5 to 37.1 g, and the tarsus length from 23.8 to 28.7 mm.

The 10 manipulated pairs initiated nests between 19 February and 23 April, laid 22 clutches, and fledged 31 young from 8 clutches (i.e. 3.1 young per pair or

1.5 young per nesting attempt). Six (60%) of the territories fledged young successfully. Thirteen of the remaining 14 nests were predated, and 1 nest was lost to inclement weather. The range of clutch-mass loss during incubation was similar to the control group (14-16%, $n = 8$). Body mass of 31 young on day 10 ranged from 26.4 to 38.0 g, and the tarsus length from 24.9 to 28.7 mm.

Examination of blood smears for hematozoa revealed that none of the 29 nestlings in the matched pairs of territories was infected. This result suggests that blood-parasite levels are not important factors determining fitness in this shrike population.

Discussion.—The importance of elevated perch sites for shrikes has been recognized (e.g. Askham 1990, Sonnerud 1992). Brooks and Temple (1990) considered perch sites an important component of the habitat-suitability-index (HSI) model that they developed for Loggerhead Shrikes. Yosef (1993) demonstrated that Northern Shrikes reacted to the introduction of perch sites by reducing their territory size an average of 12%. The results of our study confirmed that territorial Loggerhead Shrikes would react to the introduction of additional perch sites by foraging in areas made accessible for hunting and by reducing the total area defended. This result illustrates both the importance of hunting perches as a limiting resource for shrikes, and the amount of unusable habitat that is ordinarily included in a defended area.

Our results support the hypothesis that the unused area in a territory, almost fivefold greater than the minimum territory size in our study area (Yosef and Grubb 1992), is defended and not exploited and, therefore, could be manipulated to encourage more pairs of shrikes to settle. The results also support the premise that reduced territory size (and associated increase in nutritional condition of adults; Yosef and Grubb 1992) leads to increased reproductive success. Although no differences were evident in most of the

various life-history traits evaluated between control and manipulated territories, significantly more young were fledged in manipulated territories.

Our findings, coupled with those of Brooks and Temple (1990), are important in identifying potential management and conservation procedures. Areas to be managed as prime shrike habitat should include not only an appropriate prey base and nest sites, but also an abundance of hunting perches. In most shrike species, territory sizes have been shown to range widely. In our study, Loggerhead Shrike territories ranged from 0.77 to 17.6 ha. Ullrich (1971) found that Woodchat Shrike (*L. senator*) territories in Germany ranged from 4 to 12 ha. Northern Shrike territories ranged from 54.8 to 76.9 ha in Israel (Yosef 1989, Yosef et al. 1991), and from 55.4 to 357.0 ha in Idaho (Atkinson 1993). Habitat suitability for shrikes can be enhanced by introducing hunting perches, thereby allowing shrikes to forage in previously unsuitable areas. By reducing the size of existing territories, adding perches to a habitat can also increase the size of a local population by allowing more territories to be fitted into a given area.

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Behavior, Vocalizations, and Possible Relationships of Four *Myrmotherula* Antwrens (Formicariidae) from Eastern Ecuador

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The genus *Myrmotherula*, as currently recognized (Sibley and Monroe 1990), comprises 31 species of small, insectivorous antbirds, many of which have restricted geographic distributions. *Myrmotherula* reaches its greatest diversity at approximately 400-m elevation near the base of the Andes in western Amazonia between about 2°N and 13°S latitude, where up to eight species have been observed foraging with a single mixed-species flock at at least one site (pers. obs.). There is, however, a rapid drop-off in the number of species of *Myrmotherula* occurring above about 600 m in the foothills of the Andes just a few kilometers to the west. Coincident with this reduction in the number of species is a change in species composition within the genus as "foothill" species replace lowland species. Furthermore, the foothill antwrens occupy an altitudinally compressed range, being virtually absent above about 1,300 m. Thus, it is not surprising that some of these birds are among the most poorly known members of *Myrmotherula* and, indeed, of the family Formicariidae.

In the next few years, as our taxonomy of birds is increasingly determined by evidence of genetic relatedness that comes from the laboratory, there should be a corresponding body of knowledge available on the behavior and vocalizations of birds that will allow a test of our ability to use data from both fields to predict evolutionary relationships (Hackett and Rosenberg 1990). Tissue samples are fast accumulating, and molecular-based phylogenies will be worked out, in many cases, before pertinent data from the field are gathered and assimilated. In this paper I provide standardized data on the behavior and vocalizations of four little-known *Myrmotherula* antwrens from

western Napo Province, Ecuador: *M. spodionota* (Foothill Antwren); *M. behni* (Plain-winged Antwren); *M. sunensis* (Rio Suno Antwren); and *M. schisticolor interior* (Slaty Antwren).

Methods.—All observations and tape recordings were made between 27 and 30 March 1990, and between 10 and 20 January 1991 on the lower slopes of Mt. Sumaco (ca. 0°33'S, 77°44'W), an isolated, forest-cloaked mountain rising out of the lowlands to 3,900 m some 30 km east of the Andes. I observed birds with Zeiss 10 × 40 binoculars. When I located a mixed-species foraging flock containing *Myrmotherula* species (always first detected by characteristic vocalizations of one or more flock members), I made representative tape recordings of as many different vocalizations as possible, and followed the birds for as long as possible (always at least 20 min, and for as long as 2.5 h), observing foraging and other behaviors, which I summarized verbally on cassette tape. All measurements given below (heights, distances, etc.) are estimates. Terminology for foraging behavior follows Remsen and Robinson (1990). Tape recordings were made using Nagra E, Nagra 4.2, and Sony TCM-5000 recorders, and Sennheiser MKH-416 and ME-80 shotgun microphones. All recordings have been or will be archived at the Library of Natural Sounds, Cornell University, Ithaca, New York. Sonagrams were produced with "SoundEdit" of Farallon Computing, Inc., Emeryville, California, and "Canary" of the Bioacoustics Research Program at the Cornell Laboratory of Ornithology, Ithaca, New York.

Foothill Antwren (*M. spodionota*).—*Myrmotherula spodionota* (including the southern subspecies *sororia*) occurs from northeastern Ecuador south in a narrow