

obtained 10 July 1980 and deposited in the Museum of Natural History El Salvador, but unfortunately data from this specimen were not available to me. This species is not only new for El Salvador, but has not been previously reported south of Guatemala. A female of this species taken 5 miles northwest of Purulha, Baja Vera Paz, Guatemala (elev. 1200 m) appears to be the southernmost previously known record (Land and Wolf, Auk 78:94-95, 1961).

Red-faced Warbler (*Cardellina rubrifrons*).—An adult male (field no. VH-31) was obtained at El Encinal 14 February 1980 by me and is also in my private collection. W.A. Thurber mentions (pers. comm.) three earlier observations of this easily identified warbler, at Cerro Verde, Departamento de Santa Ana (13°49'N, 89°38'W): one by Thurber on 10 November 1971; another by B. L. Monroe, Jr., on 4 January 1972; and the third by a visitor, R. Greenberg on November 1976. Land (Birds of Guatemala, Livingston Publ. Co., Wynnewood, Pennsylvania, 1970:301) found this species wintering in the highlands of Guatemala, and Monroe (1968:341) found it in the western highlands of Honduras.

*Acknowledgments.*—I wish to thank every person who helped me with the manuscript, especially Dr. Walter A. Thurber, the late Dr. Eugene Eisenmann for his aid in identifying the ground-dove, and Dr. Francisco Serrano, Director of Parques Nacionales de El Salvador, for providing transportation and personnel during the field work. I thank the Martinez family at Los Planes de Montecristo for their hospitality and my wife Nicole for her encouragement.—VICTOR HELLEBUYCK, *Dept. Biology, Bishop's University, Lennoxville, Quebec J1M 1Z7, Canada. Accepted 10 Jan. 1983.*

*Wilson Bull.*, 95(4), 1983, pp. 664-667

**Territories of Rufous-sided Towhees contain more than minimal food resources.**—Birds may be defending territories that supply more than minimal resources for survival. Empirical support for this in species defending large multi-purpose territories comes from three observations. (1) During the nestling stage when food requirements are greatest, territory size is small compared to other stages of the breeding cycle (e.g., Yarrow, Auk 87: 359-361, 1970; Wasserman, *Wilson Bull.* 92:74-87, 1980). Perhaps food is not limiting, since at the time eggs hatch food is abundant and the territory size need not be large (e.g., Perrins, Ibis 112:242-255, 1970). (2) On some islands the sizes of territories are much smaller than the sizes of conspecific mainland territories (e.g., Morse, *Condor* 79:399-412, 1977). Beer et al. (*Wilson Bull.* 68:200-209, 1956) suggested that the mainland birds normally would be able to subsist in a small territory, but because of the aggressive pressures of conspecifics (unrelated to food supply) their territories are much larger than the island territories. Possibly territories are smaller on islands because of the absence of species with similar diets. (3) The breeding populations of Great Tits (*Parus major*) during one breeding season were considerably higher than they were during any other year (Lack, *Population Studies of Birds*, Clarendon Press, Oxford, England, 1966). Lack argued that populations could not have been limited by resources in other years. Tompa (Auk 79:687-697, 1962) reported a similar circumstance in Song Sparrows (*Melospiza melodia*); in one year breeding density of sparrows was greater than average with no apparent change in food availability. Knapton and Krebs (*Can. J. Zool.* 52:1413-1420, 1974) presented evidence indicating that size of territories is proximately determined by the number of individuals attempting to settle and not by food availability.

Researchers suggesting birds defend territories that supply just enough resources for survival usually point out that: (1) territory size is inversely related to food availability (e.g., Stenger, Auk 75:335-346, 1958); and/or (2) breeding density is directly related to food availability (e.g., Zach and Falls, *Can. J. Zool.* 53:1669-1672, 1975). A few field experiments have

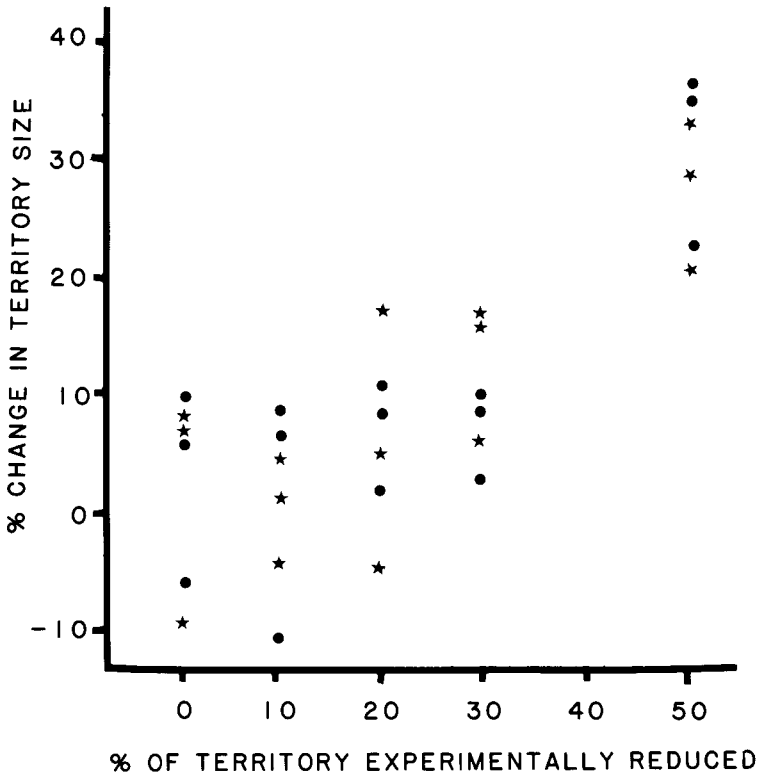


FIG. 1. Percent change in territory size before and after manipulation during the nestling stage. Circles indicate males and triangles females. With the exception of the 10% group, each symbol represents the percent change in area between two 100-min periods of foraging observations, one before and one after manipulation. The percentages used for the 10% group are based on mean territory sizes before and after manipulation (Table 1).

involved an attempt to manipulate food availability. Miller et al. (pp. 323–335 in *Animal Populations in Relation to Their Food Resources*, Blackwell, Oxford, England, 1970) with the Red Grouse (*Lagopus lagopus*) and Krebs (*Ecology* 52:2–22, 1971) with Great and Blue (*P. caeruleus*) tits found that after food was added there was either a decrease or no change in population density (territory size was not measured directly).

When Franzblau and Collins (*Oecologia* 46:164–170, 1980) added food to the territories of Rufous-sided Towhees (*Pipilo erythrophthalmus*) (increasing invertebrate biomass by approximately 96%) they found no change in territory size and no difference between the sizes of five experimental territories and five control territories. They concluded that size of territory was not a function of the immediate food supply.

In the present study I eliminated certain amounts of food in the territories of breeding pairs of Rufous-sided Towhees. The lack of a significant increase in territory size or decrease in breeding success after treatment suggests that these territories contained more than minimal food resources.

**TABLE 1**  
**TERRITORY SIZES BEFORE AND AFTER 10% OF THE TERRITORY WAS EXPERIMENTALLY REDUCED**

	Before $\bar{x} \pm SE (N)$	After $\bar{x} \pm SE (N)$	Mann-Whitney <i>U</i> -test <sup>a</sup> <i>U</i> -values
Nestling stage			
Pair 1 male	4120 ± 840 (3)	4460 ± 1130 (3)	6
female	3130 ± 500 (3)	3270 ± 650 (3)	5
Pair 2 male	2970 ± 640 (4)	2660 ± 610 (3)	7
female	1260 — (1)	1270 ± 90 (2)	
Pair 3 male	2810 ± 330 (7)	2990 ± 300 (4)	17
female	4880 ± 1350 (3)	5660 ± 930 (3)	7
Fledgling stage			
Pair 1 male	6970 ± 1190 (6)	6540 ± 1280 (3)	9
female	2400 ± 700 (4)	3770 ± 930 (6)	15

<sup>a</sup> All comparisons  $P > 0.30$ .

*Methods.*—During the spring and summer of 1979, 1980, and 1981, I observed 16 breeding pairs of Rufous-sided Towhees at the Massachusetts Broadmoor/Little Pond Wildlife Sanctuary in South Middlesex Co., Massachusetts. I divided each territory into 10 by 10 m quadrats and recorded a bird's predominant activity and location, placing its position on a grid. I estimated territory size by using the computer program of Koepl et al. (J. Mammal. 56:81-90, 1975). The program gives an ellipse for a series of observations. One observation each minute for 100 min of foraging represented estimates of territory size before and after manipulation.

The breeding pairs of towhees were selected so that each had a territory that was not completely constrained by adjacent territories. On at least one border there was room for expansion into unused habitat.

Ten, 20, 30, or 50% of available feeding area in each territory was made inaccessible to the birds by randomly placing 10-m<sup>2</sup> clear polyethylene sheets and/or crop-protection netting in quadrats (making invertebrate prey unavailable to the birds). The birds seemed to forage uniformly within each 100-m<sup>2</sup> quadrat. For the manipulations one, two, three, or five 10-m<sup>2</sup> sections were eliminated from each quadrat by choosing section positions from a random numbers table (each quadrat was composed of ten 10-m<sup>2</sup> sections). The placing of the sheets and treatments were applied on days 4-6 of the nestling stage of 15 pairs of birds and during the fledgling stage of one pair. Days 1-3 in each stage served as controls for the respective manipulations. I used a Kruskal-Wallis test to determine if there was a difference in percent change in territory size during the nestling stage among the 0, 10, 20, 30, and 50% groups.

For the situation where 10% of the territories was made unavailable to territory holders I used a Mann-Whitney *U*-test to compare the territory sizes of individual birds (male and female of three pairs, Table 1) before and after manipulation (the numbers of 100-min replicates for the other territory reduction groups were too small to test in this fashion). To test for a difference between male and female territory size before manipulation (days 1-3 in each nestling stage, 15 pairs of birds) I used a Wilcoxon paired-sample test.

*Results.*—There was a significant difference in percent change in territory size during the nestling stage among the 0, 10, 20, 30, and 50% groups (Fig. 1; Kruskal-Wallis test,  $P <$

0.01). Birds whose available foraging area was reduced by 50% increased the size of their territories to a greater degree than the other four groups ( $P < 0.05$ , nonparametric multiple comparison; Zar, *Biostatistical Analysis*, Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 1974). There was no significant difference in percent increase in territory size among the 0, 10, 20, and 30% groups.

After 10% of the available foraging area was made inaccessible to the birds in the nestling stage there was no significant change in territory size for either the male or female in the three pairs studied (Table 1). On average males increased their territories 1.4% ( $N = 3$ ) and the females 7.1% ( $N = 3$ ). Before manipulation average male territories ( $\bar{x} \pm SD = 5220 \pm 1450 \text{ m}^2$ ,  $N = 15$ ) were not statistically significantly larger than female territories ( $\bar{x} \pm SD = 4460 \pm 1660 \text{ m}^2$ ,  $N = 15$ ). In the pair studied during the fledgling stage there was a 6.1% decrease in the size of the male's territory and 57.1% increase in the size of the female's territory (Table 1).

*Discussion.*—Hinde (*Behaviour Suppl.* 2, 1952) found that when winters in England are unusually mild, Great Tits remain territorial; but if conditions become more severe, they form social groups. On warm days in late winter they will, at least temporarily, settle within their territories, possibly responding to the lowered energy requirements of mild days. Carpenter and MacMillen (*Science* 194:639–642, 1976) found that Hawaiian Honeycreepers (*Vestiaria coccinea*) shifted from territorial to non-territorial states in response to size of nectar supply and competitive pressure. Alterations of Rufous-sided Towhee territories were made when energy demands should be highest and response to limitation of food source should occur. Fluctuations in territory size from one stage in the breeding cycle to another are common in many species (e.g., Stefanski, *Condor* 69:259–267, 1967).

There have been few experimental, manipulative avian studies which attempt to determine if birds defend territories that supply more than minimal food resources. Featherstone (M.Sc. thesis, Univ. Toronto, Toronto, Ontario, 1966), using pesticides, decreased the foraging area of individual Ovenbirds (*Seiurus aurocapillus*) by 42% and found that the birds increased the size of their territories 38%. He concluded that the size of Ovenbird territories is at least partially determined by the amount of food present.

My results indicate that when 0, 10, 20, or 30% of the territories was made unavailable an adequate food supply was still available. Only when 50% of the territory was made unavailable was there a substantial increase in the territory size. There are at least two explanations for this result. One is that the function of territoriality is more than the procurement of a food resource. Territorial behavior in the Rufous-sided Towhee may also be a means of preventing sexual interference from conspecifics. An alternative, but not a mutually exclusive one, is that the birds are defending territories that contain more food than they can consume as insurance against a bad year.

*Acknowledgments.*—This research was supported by a Public Health Service Grant (MH 33824-01). I would like to thank B. Lund and the Massachusetts Audubon Society for their cooperation during the course of this research. For help of various kinds I would like to thank P. V. August, R. H. Tamarin, L. Whiteside, and R. Zach.—FRED E. WASSERMAN, *Dept. Biology, Boston Univ., Boston, Massachusetts 02215. Accepted 31 Aug. 1982.*

*Wilson Bull.*, 95(4), 1983, pp. 667–669

**The shoulder-spot display in male Blue Grouse.**—A “shoulder-spot” display has been described for both males and females of several species of grouse (Lumsden, *Living Bird* 9:65–74, 1970). The shoulder spot is formed by exposing the white underwing coverts at the proximal end of the humerus on the upper surface of the wing (Lumsden 1970). Movement of the patagial skin may also be important in effecting this display (Carbutt,