SHORT COMMUNICATIONS

Sexual Differences in the Spatial Distribution of Foraging in White-throated Sparrows (Zonotrichia albicollis)

FRED E. WASSERMAN

Department of Biology, Boston University, Boston, Massachusetts 02215 USA

There are a number of reasons that male and female birds may utilize different areas of their territories for foraging. One reason is to partition the territory for efficient exploitation of available resources by one sex (Kamil and van Riper 1982). Alternatively, males and females may forage in different areas because selection favors a division of labor in parents (Morse 1968; Robins 1971a, b; Williamson 1971; Holmes et al. 1978; Franzreb 1983). The purpose of this study was to determine if the sexes of the Whitethroated Sparrow (*Zonotrichia albicollis*) partition their foraging area.

During the springs of 1974 (1 pair), 1975 (4 pairs), 1976 (2 pairs), 1979 (1 pair), and 1984 (2 pairs), I observed 10 pairs of White-throated Sparrows on their breeding grounds in Danbury (2 study areas), Wilmot, and Cheshire counties, New Hampshire. I observed 2 pairs throughout their entire breeding cycle (Tables 1 and 2) and 8 additional pairs during various breeding stages (Table 3). The nestlings of pair 1 were taken by a predator and a renesting took place. All birds were color banded and recognized by the color bands or other distinguishing characteristics. Each of the 4 study areas was divided into 10×10 -m quadrats, and individual birds were followed on their territories for continuous time periods from approximately 30 m. I recorded the location of foraging for each 1-min observation period. Almost all observations were made between 2 and 5 h after sunrise.

To establish where in the territory the birds spent their time, I considered five concentric regions around the geographic activity centers (the average x-y coordinate of all behavioral observations) of each stage of the breeding cycle. The first region consisted of the 10×10 -m quadrat containing the geographic activity center plus the 8 quadrats surrounding the activity center. The second region consisted of the 16 quadrats surrounding but not including the first region. The third region incorporated the 24 quadrats encircling these 16 squares, and the fourth region was formed by the 32 quadrats surrounding the first three regions. The fifth region covered all foraging that occurred outside the first four concentric areas. For one pair observed during the entire breeding

Sex and	Stageª										
region	Р	М	NB	I	Ν	М	NB	I	Ν	F	Total ^f
Male											
1	31 ^b	27	13	24	44	18	55	40	44	20	29
2	36	24	21	38	26	35	24	34	25	20	28
3	16	20	30	21	16	25	9	17	18	28	21
4	9	13	19	10	10	11	3	7	9	18	12
5	8	16	18	7	4	11	10	2	4	13	11
	(800) ^c	(1,800)	(1,200)	(1,000)	(500)	(300)	(400)	(800)	(700)	(500)	(8,000)
		NS ^a	↓e	\downarrow	Ţ	Ť	NS	NS	NS	NT	Ļ
Femal	e										
1	_	27	27	74	58	13	54	40	51	37	35
2	_	25	25	13	21	21	33	36	23	31	25
3	_	22	22	6	12	31	4	18	18	12	19
4	—	11	11	4	9	25	9	6	3	3	11
5		15	15	3	0	10	0	0	5	17	10
		(1,400)	(800)	(400)	(200)	(200)	(200)	(400)	(100)	(100)	(3,800)

 TABLE 1. The spatial distribution of foraging behaviors for pair 1.

* P = premating, M = mating, NB = nest building, I = incubation, N = nestling stage, F = fledgling stage. * Percentage of total observations observed for each stage in each of the five regions.

^c Total number of observations for each stage.

 $^{\rm d}$ NS = no significant difference between sexes in foraging distributions; NT = significant difference in distribution but no trend toward the center for either male or female.

* Arrows point to the sex whose foraging was significantly more concentrated at the center.

^f Total values were calculated by considering each stage separately and summing over all stages for each region.

Sex and _	Stage								
region	М	NB	Ι	Ν	F	Tota			
Male									
1	62	50	45	28	47	37			
2	22	30	35	29	33	30			
3	16	18	16	29	15	23			
4	0	2	4	14	5	10			
	(73)	(189)	(464)	(1,220)	(179)	(2,125)			
	NS	NS	Ţ	Ţ	1	ł			
Female					·	•			
1	69	52	48	59	75	60			
2	26	32	39	18	11	20			
3	5	12	9	15	6	13			
4	0	4	4	8	8	7			
	(61)	(116)	(252)	(1,461)	(266)	(2,156)			

TABLE 2. The spatial distribution of foraging behaviors for pair 2.*

^a Symbols and data are defined in Table 1.

season (Table 2) only four concentric regions were considered. In this study the nests were located within 25 m of the geographic activity center.

To determine if foraging activities were skewed toward the center of the territory, activity distributions were compared with the distribution of equal occurrence per unit area in each region. This analysis compensates for the inequality of the areas in the five regions. To compute a unit area for the indefinite fifth region, the total number of foraging observations outside of the first four regions was divided by 40 quadrats. Conformity to the equal occurrence distribution was tested by the Kolmogorov-Smirnov one-sample test (Siegel 1956). I used a Kolmogorov-Smirnov two-sample test (Siegel 1956) to compare the spatial distributions of male and female foraging in each stage of the breeding cycle. If there was a significant difference (P < 0.05) in the cumulative distributions, I determined if the male or female consistently foraged closer to the activity center.

Male and female foraging was concentrated toward the center of the territory in all stages of the breeding cycle (P < 0.05; Kolmogorov-Smirnov onesample test). Female foraging occurred significantly closer to the activity center than did male foraging (P < 0.05; Kolmogorov-Smirnov two-sample test; Tables 1–3). When the stages of the breeding cycle were considered separately, this was particularly evident during the incubation and nestling stages (Tables 1– 3), except during the renesting of pair 1. The males did not appear to avoid actively the areas close to the nest where the females concentrated their foraging activity. Rather, the partitioning seemed to be more passive.

Both sexes skew foraging toward the center of the territory. The female tends the nest there and the male sings close to the territory center (Wasserman 1982). During the incubation and nestling phases of the breeding cycle, however, females forage closer to

the centers of the territories than males. During the incubation phase the females, but not males, might be expected to be central-place foragers because of their nesting tenacity. During the nestling stage both males and females feed the young and both sexes should be central-place foragers. Females spend considerable time brooding nestlings, however, and may concentrate their foraging activity closer to the nest than males. In a number of species (Morse 1968, Power 1980) incubating females forage more rapidly than do males, suggesting that females may be under stricter time and energy constraints during this period. By foraging closer to the nest, females limit the amount of time off the nest and the time spent foraging. This presumably decreases the likelihood of predation on the nest. Also, by spending more time on the nest they may speed the incubation process.

In a number of species male-female niche partitioning may be a consequence of the male foraging where it sings, often on the periphery of its territory (Morse 1968; Williamson 1971; Robins 1971a, b; Franzreb 1983). This does not appear to be the situation in White-throated Sparrows because both males and females are ground-foraging birds and because males sing closer to the center of the territory than they forage (Wasserman 1982). In some species, like the Mountain Bluebird (*Sialia currucoides*), both sexes show a similar decline in foraging effort with increasing distance from the nest (Power 1980). One possible explanation for the similarity is that the food supply is adequate and the animals derive no benefit from partitioning the habitat.

Alternatively, partitioning the foraging area may reduce predation on nests by decreasing the activity of adults around the nest site during the incubation and nestling stages. The success rate of White-throated Sparrow nests is approximately 50% (Knapton et al. 1984). Any behavior that would reduce predation around the nest would be favored. In White-crowned

Sex and	Stage									
region	М	NB	I	N	F	Total				
Male				· · · · · · · · · · · · · · · · · · ·						
1	38	32	43	40	30	37				
2	25	26	22	33	31	27				
3	19	23	19	21	18	20				
4	14	11	11	4	13	11				
5	4	8	5	2	8	5				
	(1,262)	(625)	(840)	(783)	(509)	(4,019)				
	NS	1	1	1	NT	1				
Female		•	•	·		•				
1	39	45	52	59	40	46				
2	27	24	28	21	26	25				
3	21	19	13	15	19	18				
4	10	7	4	4	8	7				
5	3	5	3	1	7	4				
	(1,094)	(513)	(452)	(520)	(367)	(2,946)				
No. pairs										
observed	6	5	5	5	4	8				

TABLE 3. The spatial distribution of foraging for 8 pairs of White-throated Sparrows.^a

* Symbols and data are defined in Table 1.

Sparrows, both sexes concentrated their foraging toward the center of the territory in all stages of the breeding cycle, but females foraged significantly closer to the activity center than did males. I conclude that females forage closer to the nest to limit the amount of time off the nest and the time spent foraging.

Grants from the United States Public Health Service (#MH 33824-01) and Boston University supported this research. I wish to thank J. Davies, R. W. Knapton, J. L. Zimmerman, A. Hart, and C. van Riper III for their comments on an early draft of the manuscript.

LITERATURE CITED

- FRANZREB, K. E. 1983. Intersexual habitat partitioning in Yellow-rumped Warblers during the breeding season. Wilson Bull. 95: 581-590.
- HOLMES, R. T., T. W. SHERRY, & S. E. BENNETT. 1978. Diurnal and individual variability in the foraging behavior of American Redstarts (Setophaga ruticilla). Oecologia 36: 141-149.
- KAMIL, A. C., & C. VAN RIPER III. 1982. Within-territory division of foraging space by male and

female Amakihi (Loxops virens). Condor 84: 117-119.

- KNAPTON, R. W., R. V. CARTER, & J. B. FALLS. 1984. A comparison of breeding ecology and reproductive success between morphs of the Whitethroated Sparrow. Wilson Bull. 96: 60-71.
- MORSE, D. H. 1968. A quantitative study of foraging of male and female spruce-woods warblers. Ecology 49: 779-784.
- POWER, H. W. 1980. The foraging behavior of Mountain Bluebirds with emphasis on sexual foraging differences. Ornithol. Monogr. No. 28.
- ROBINS, J. D. 1971a. Differential niche utilization in a grassland sparrow. Ecology 52: 1065-1070.
- ——. 1971b. A study of Henslow's Sparrow in Michigan. Wilson Bull. 83: 39–48.
- SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. New York, McGraw-Hill.
- WASSERMAN, F. E. 1982. The spatial distribution of singing and foraging in the territories of Whitethroated Sparrows. Can. J. Zool. 60: 2757-2760.
- WILLIAMSON, P. 1971. Feeding ecology of the Redeyed Vireo (Vireo olivaceous) and associated foliage-gleaning birds. Ecol. Monogr. 41: 129–152.

Received 13 March 1985, accepted 16 October 1985.