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TERRITORIAL BEHAVIOR IN A PAIR OF WHITE-THROATED SPARROWS

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The importance of territorial behavior lies in the survival and reproductive value gained by the animal using it. Not all territories bring the same benefits, but there is good evidence that the survival value is often in the form of the procurement of a food resource (e.g., Lack 1955, 1958, 1964; Stenger 1958; Stenger and Falls 1959; Schoener 1968; Brown 1969; Brown and Orians 1970; Orians 1971; Gill and Wolf 1975; Zach and Falls 1975; Gass et al. 1976; Morse 1976). This is particularly apparent in the case of individual birds holding winter territories far from the breeding grounds (Lederer 1977a, b; Salmonson and Balda 1977). For other birds territorial behavior may be directly related to the procurement of a mate and the protection of the pair from the influence of conspecifics (e.g., Tinbergen 1936; Odum 1941; Conder 1949; Hinde 1952, 1956; Marler 1956; French 1959; Samson 1976). In still other species territoriality may serve as a spacing mechanism, acting to reduce predation or lower mortality due to disease (Hinde 1956).

The possible functions of territoriality are diverse, and simple answers about territorial function are unlikely to be found (Hinde 1956, Schoener 1968, Brown and Orians 1970). Only through concentrated surveillance of individual animals is the ethologist able to unwind the paradigms of territoriality. In this paper I quantify changes in territorial behavior throughout the season in 1 pair of White-throated Sparrows (*Zonotrichia albicollis*). The direct response of the male to his mate's behavior lends support to hypotheses concerning the sexual functions of territoriality, although the possibility that territoriality also serves other functions should not be dismissed.

METHODS

White-throated Sparrows form monogramous pair bonds and activities of the pair occur within the home area during the breeding season (Lowther and Falls 1968, Type A territory as defined by Nice 1937). In Wilmot Co., New Hampshire, males arrive on the breeding grounds in mid-April and females arrive approximately 2 weeks after the males. Here, White-throated Sparrows have their densest breeding populations in semi-open fields where the main vegetation is a low spreading evergreen (*Juniperus communis*) about 1 m tall and often several meters in diameter.

I divided a square area into 400 10-by-10 m quadrats. Within this marked region I observed 1 pair of White-throated Sparrows. Two mated pairs occupied adjacent areas. I distinguished all individuals by color bands or distinctive markings.

The male's behavior was classified into 6 general categories.

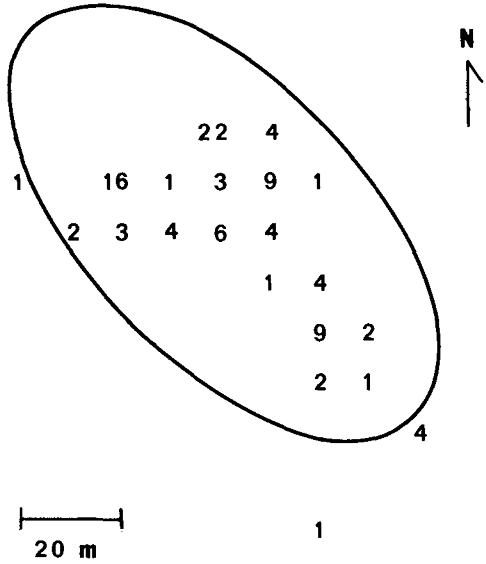


FIG. 1. Ninety-five percent confidence ellipse for the first 100-min sample of male singing during the premating stage. Numbers correspond to the number of minutes the male was observed singing in each quadrat. The area of the ellipse equals 4670 m^2.

(1) *Foraging.*—The male foraged primarily on the ground. In the early spring he fed on spore capsules of the hair cap moss (*Polytrichum* sp.) and later in the season he scratched at the ground and uncovered insects. Occasionally he jumped from the ground and captured flying insects.

(2) *Advertising song.*—The song consists of a series of tonal notes combined in a definite pattern. He sang full loud song from a number of high song perches, typically elevating his head with his beak vertically upward, perhaps allowing optimal spherical spread of the sound.

(3) *Alert defensive posture.*—He performed defensive posture from a perch, directing it toward conspecifics. His head and thorax feathers were fluffed, giving the illusion of increased size. Quite often, chasing or supplanting of the conspecific preceded or followed defensive posture and chipping vocalizations (described by Lowther and Falls 1968 as "pink," "chup-up" and trills) commonly accompanied the behavior.

(4) *Whisper song.*—The pattern of whisper song was identical to that of advertising song, but was of a lower amplitude and was given from the ground.

(5) *Chases.*—Birds flew after conspecific strangers or neighbors.

(6) *Resting.*—The male sat on the ground and showed no overt activity.

In this analysis, I will consider only foraging behavior of the female. She foraged almost exclusively on the ground. I calculated the rate of movement in m per min for both the male and female. This measurement for the male does not include minutes when he was singing, in defensive posture, or in chase.

Between 5 May and 4 August 1974, I observed the male for 197 h and the female for 64

h. Singing of advertising song was categorized into morning (07:00–12:00) and afternoon (12:00–18:00) activity. Behavioral changes accompanying different stages of the breeding cycle influenced the ease with which individuals could be located and followed. The male seemingly habituated to me and occasionally approached to within 1 m of me. The female remained more wary. During each min I recorded the predominant activity and the location of the bird I was observing. Whenever possible I recorded the female's location with respect to the male.

To estimate the area utilized by the birds I used the computer program of Koeppl et al. (1975). The program is advantageous because it: (1) gives a 95% confidence ellipse (Fig. 1); and (2) rotates the axes of the ellipse and gives a measure of area which is independent of the original grid and axes.

For utilized area (male singing, male foraging and female foraging areas) and for the various activities (singing, chases, defensive posture, etc.) successive 100-min observation periods comprised the within-nesting stage replication. To locate differences among stages I used 1-way analysis of variance (ANOVA). I used Dayton's (1970) 2-way ANOVA for unequal cell size on 3 sets of data. In these 3 analyses, nesting stage was 1 independent variable while the other independent variable was sex (male and female foraging area) or activity (male singing and foraging areas) or time (morning and afternoon singing). When an ANOVA indicated a significant difference ($P < 0.05$), I tested differences between subsequent stages using the Least Significance Difference (LSD, 2-tailed test; Snedecor and Cochran 1972). In the results section I use the terms increase or decrease to imply that there was a significant change ($P < 0.05$).

To return area measurements to a linear scale, I applied a square root transformation to the original values ($\sqrt{X} = X'$). To normalize the data when group variances were proportional to the means and some of the observations were 0 (defensive posture, whisper songs, chases and resting) I used a $\sqrt{X + 0.5}$ transformation (Zar 1974). I report back-transformed means ±SE (e.g., the mean plus SE equals $[X' + SE']^2$).

RESULTS

Comparison of the independent variables, nesting stage (Table 1) and activity (male foraging and male singing area), indicated that the area used by the male was different between stages (2-way ANOVA; $F = 2.83$; df = 9, 86; $P < 0.01$). The area in which the male sang (Fig. 2A) was smaller than the area in which he foraged (Fig. 2B; $F = 6.06$; df = 1, 86; $P < 0.001$). The interaction term was non-significant. Considering the means of each stage, male foraging area and male singing area were highly correlated ($r = 0.83$, df = 8, $P < 0.01$). From nest-building to incubation in the first nesting, male foraging area decreased.

Comparison of the independent variables, nesting stage (from mating of the first nesting until fledgling) and sex (male and female foraging area), indicated that the area used for male and female foraging was different between stages (2-way ANOVA; $F = 4.30$; df = 8, 92; $P < 0.001$). The male foraged (Fig. 2B) in a larger area than the female (Fig. 2C; $F = 4.78$; df = 1, 92; $P < 0.05$). The interaction term was non-significant. Considering the mean areas of each of the stages, male foraging area and female foraging area were highly correlated ($r = 0.87$, df = 7, $P < 0.01$). Female

TABLE 1
STAGES IN THE NESTING CYCLE

Stage	Description	Date	
		First nesting	Renesting
Premating (P)	Arrival of the male until the arrival of the female	5–14 May	
Mating (M)	Arrival of the female until nest-building	15–25 May	15–18 June
Nest-building (NB)	Beginning of nest-building until the beginning of incubation	26 May–1 June	19–21 June
Incubation (I)	Female incubating the eggs	2–10 June	22–30 June
Nestling (N)	Eggs have hatched and both parents feed the young	11–14 June	1–10 July
Fledgling (F)	Young leave the nest and the parents feed the fledglings	Predation[1]	11 July– 4 August

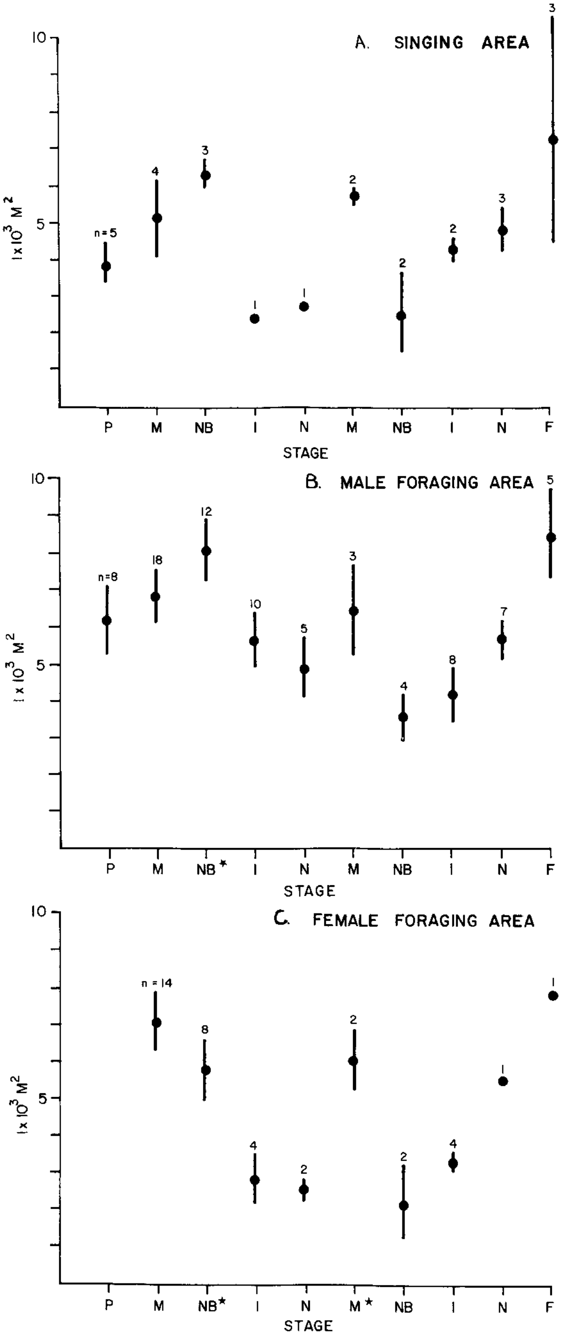
[1] On 14 June the nestlings were taken by a predator.

foraging area decreased when she began incubating eggs during the first nesting. After the predation on the first nest and the mating stage of renesting, female foraging area decreased.

Comparison of the independent variables, nesting stage (premating to incubation of renesting) and time (rate of morning and afternoon singing), indicated that the rate of advertising song was different between stages (2-way ANOVA; F = 7.72; df = 7, 92; $P < 0.001$). Rate of singing in the morning (Fig. 3A) was greater than the rate of singing in the afternoon (Fig. 3B; F = 8.82; df = 1, 92; $P < 0.01$). The interaction term was nonsignificant.

Once the female arrived, male singing in the morning decreased. During the mating stage of the renesting (following predation on the first nest), singing increased as the pair established a new area for renesting. In renesting, singing was lower in the afternoon once the female began incubation. Finally, as the young fledged, singing increased in the morning.

The rate of defensive posturing varied between stages (Fig. 4A; 1-way ANOVA; F = 10.99; df = 9, 102; $P < 0.001$). I first observed it during the mating phase when the female arrived on the breeding grounds. I did not include defensive posture directed toward the female in the calculation of the results so as not to confuse the establishment of the pair bond with a defensive behavior. After mating, defensive posture decreased and did not increase until after the predation on the first nest. Once again, after


A. SINGING AREA
10
5
1 x 10³ M²
n=5
4
3
1
1
2
2
2
3
3
P M NB I N M NB I N F
STAGE
B. MALE FORAGING AREA
10
5
1 x 10³ M²
n=8
18
12
10
5
3
4
8
7
5
P M NB* I N M NB I N F
STAGE
C. FEMALE FORAGING AREA
10
5
1 x 10³ M²
n = 14
8
4
2
2
2
4
1
1
P M NB* I N M* NB I N F
STAGE

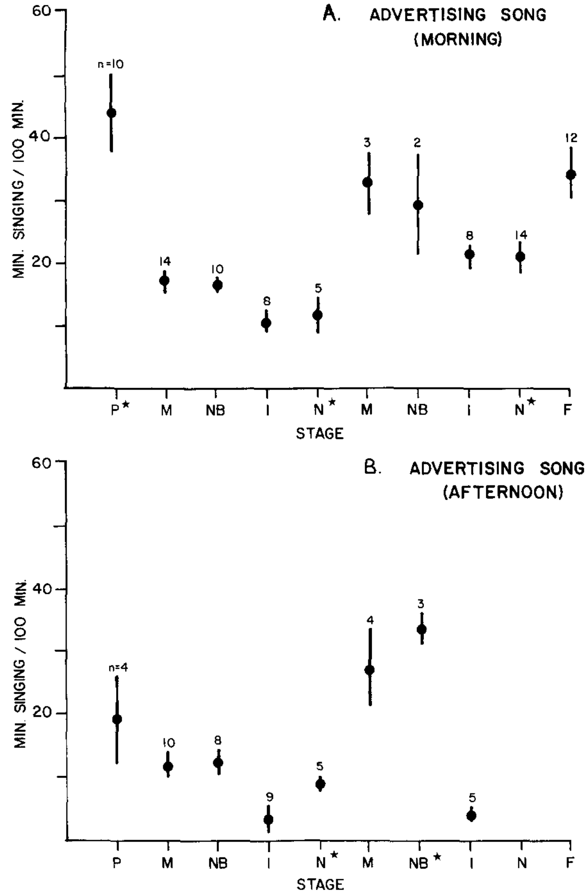


FIG. 3. Average number of min per 100-min of observation (±SE) that the male was involved in advertising song in (A) morning (07:00–12:00) and (B) afternoon (12:00–18:00) in each stage of the nesting cycle. If the male sang at least once during the 1-min interval he was considered singing for that min. N and stars defined as in Fig. 2.

the mating period ended there was a decrease in the number of minutes spent in defensive posture. After the young left the nest defensive posture decreased.

There was no difference between stages in the rate at which chases

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FIG. 2. Average area of the 95% confidence ellipses (±SE) used to determine (A) male singing area, (B) male foraging area and (C) female foraging area for each stage of the nesting cycle. N equals the number of 100-min samples used to estimate area utilized in each stage. A star indicates stages in which mean foraging area was significantly different from the mean area of the stage immediately following.

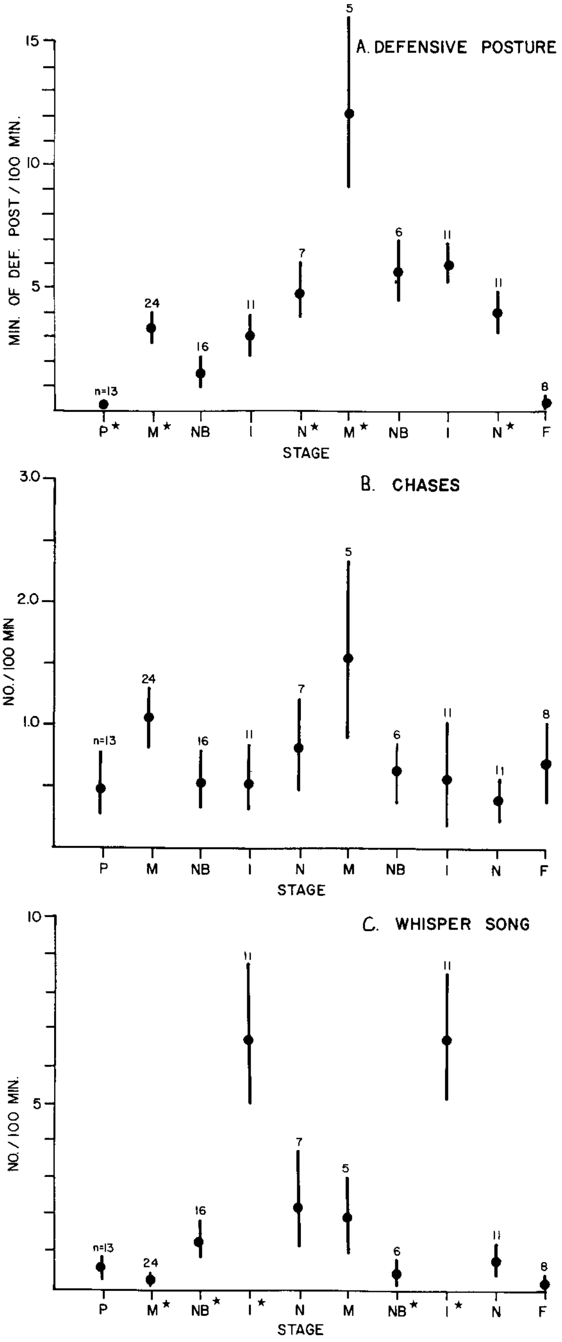
A. DEFENSIVE POSTURE
MIN. OF DEF. POST / 100 MIN.
15
10
5
n=13
24
16
11
7
5
6
11
11
8
P★
M★
NB
I
N★
M★
NB
I
N★
F
STAGE
B. CHASES
NO./100 MIN
3.0
2.0
1.0
n=13
24
16
11
7
5
6
11
11
8
P
M
NB
I
N
M
NB
I
N
F
STAGE
C. WHISPER SONG
NO./100 MIN.
10
5
n=13
24
16
11
7
5
6
11
11
8
P
M★
NB★
I★
N
M
NB★
I★
N
F
STAGE

TABLE 2

FREQUENCY OF WHISPER SONGS GIVEN WHILE THE MALE AND FEMALE WERE IN THE SAME QUADRAT

	No. of whisper songs given when the male and female were in the	
First nesting	Same quadrat	Different quadrats
Observed	20	124
Expected	34.15[1]	109.85
	$\chi^2 = 7.69$, df = 1, $P < 0.01$	
Renesting	Same quadrat	Different quadrats
Observed	12	120
Expected	26.53	105.46
	$\chi^2 = 9.96$, df = 1, $P < 0.01$	

[1] The % of time the male and female were in the same quadrat was calculated only for days in which the male sang whisper song; in the first nesting this was 23.7% (based on 3264 min of observation), and in renesting 20.1% (based on 1995 min).

occurred (Fig. 4B; 1-way ANOVA; F = 0.83; df = 9, 102; $P > 0.05$). The highest rates of chases per min occurred in the mating stages.

There was a difference in the number of whisper songs given per 100 min across stages (Fig. 4C; 1-way ANOVA; F = 11.83; df = 9, 102; $P < 0.001$). After the initial mating period and the establishment of the pair bond there was an increase during incubation. After incubation whisper singing decreased as the parents fed the young. During renesting the highest frequency of whisper singing occurred in the period of incubation. In the nestling period whisper singing decreased.

Whisper songs were given most frequently in the female's absence. This was true during the first nesting as well as during renesting (Table 2).

There was a difference between stages in the rate at which the male rested (1-way ANOVA; f = 3.36; df = 9, 102; $P < 0.01$). I observed the male resting in only 2 stages, incubation and the nestling stage of the first nesting attempt. There was an increase in the rate of resting during incubation and a decrease after the nestling stage. I never saw the female involved in resting behavior off the nest.

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FIG. 4. Average number (±SE) of (A) min spent in defensive posture, (B) chases and (C) whisper songs per 100 min in each stage of the nesting cycle. N and stars defined as in Fig. 2.

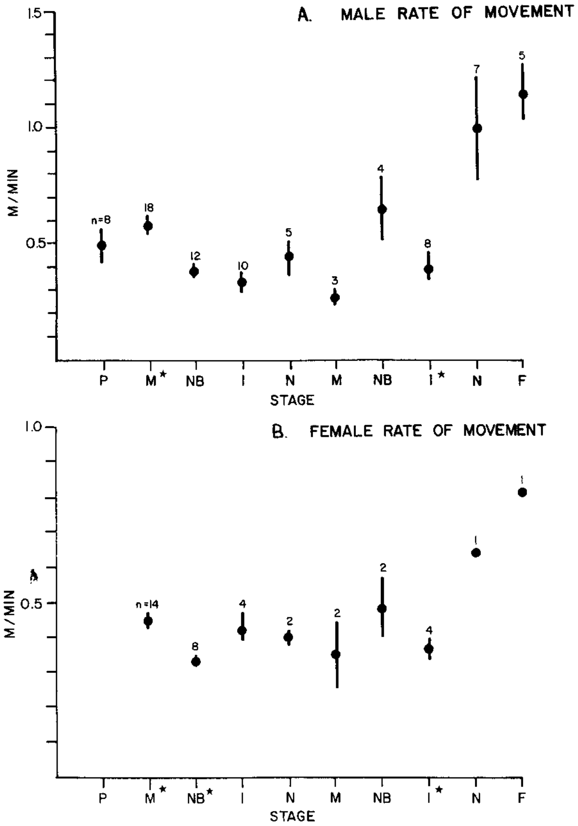

FIG. 5. Average rate of movement (±SE) for the (A) male and (B) female in each stage of the nesting cycle. Calculations of means for the male do not include minutes when he was recorded either singing in defensive posture or in chase. N and stars defined as in Fig. 2.

Rate of male movement (Fig. 5A) was different between stages (1-way ANOVA; F = 8.03; df = 9, 70; $P < 0.001$). It decreased after the mating stage of the first nesting and showed an increase in the nestling stage of the renesting. The female's rate of movement (Fig. 5B) was also different between stages (1-way ANOVA; F = 6.91; df = 8, 29; $P < 0.001$). She demonstrated the same pattern as the male with the additional effect of an increase in rate of movement during the incubation stage of the first nesting attempt. Mean rates of male and female movement in each stage were highly correlated ($r = 0.93$, df = 8, $P < 0.001$).

The likelihood of finding male and female in the same quadrat was different between stages (Fig. 6; 1-way ANOVA; F = 7.25; df = 8, 43; $P < 0.001$). The male spent more than 50% of his time in the same quadrat

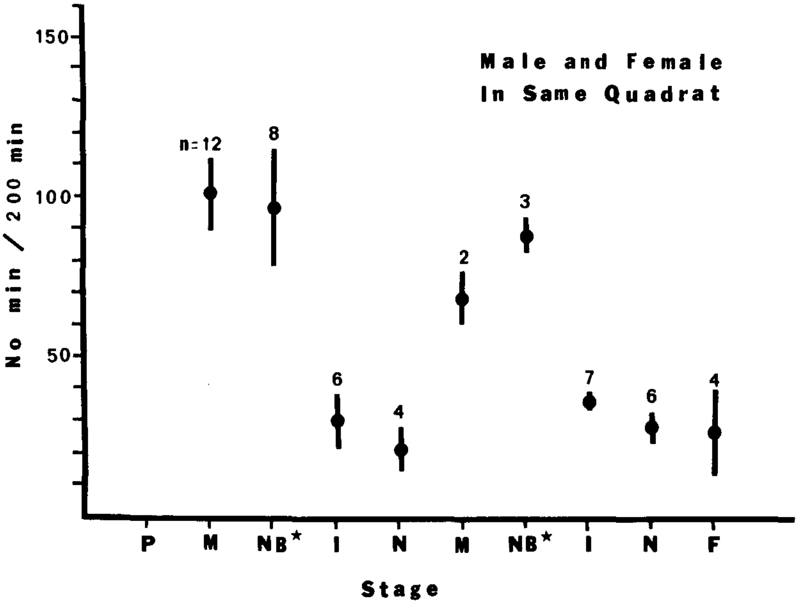

FIG. 6. Average number of min out of 200 (±SE) during which the male and female were in the same quadrat in each stage of the nesting cycle. Stars defined as in Fig. 2. N equals the number of 200-min samples used to determine means.

as the female when she arrived on the breeding grounds. When the female began incubation the amount of time the male and female were together decreased. Following predation of the first nest the male again began a close association with the female until incubation. During incubation male-female association decreased.

DISCUSSION

Upon viewing the overall performance of these 2 birds it is now appropriate to show how the behavior of each complements and interacts with that of the other. The male was continuously chased by conspecifics when he appeared on the breeding grounds. He did not abandon his territory, and after 1 day chases subsided. Singing of advertising song steadily increased, reaching a peak the day before the female appeared and subsequently decreasing (Fig. 3).The decline of singing after female arrival in many species, including the White-throated Sparrow (Wasserman 1977), has suggested to some (e.g. Catchpole 1973, Marshall 1964, Verner 1965) that mate attraction may be one function of song.

When the female arrived the male's activity changed considerably. He increased the size of his foraging and singing areas, began to show defensive behavior and increased his rate of movement. He spent more than 50% of his time in close association with the female. During encounters at territorial boundaries he prevented encroachment upon the female by placing himself between her and a neighboring male. As he accompanied the female into a neighbor's territory he was often chased by the neighbor. In short, the male was in an alert, aggressive state, making territorial alterations to accommodate the female. As Emlen (1957) pointed out, the use of the term "a defended area" is erroneous because there is "no evidence that the area is the object of the aggressive behaviour." Similarly, it should not be said that the male is defending the female; however, it is clear the major objectives of the male are to establish the pair bond and to reduce the chances of being cuckolded. He is accomplishing these objectives with the high energy demand that aggressive behavior requires. At the same time the female is being introduced to his territory. The nest was built on the ground under juniper shrubbery, within 10 m of the center of male activity, before female arrival. During incubation both the male and female decreased their foraging areas. The male sang less and his rate of defensive posturing and chasing remained low. The territorial system appeared to be more stable than before; this stability and the smaller foraging areas were most likely attributable to the female being close to the nest and incubating the eggs. However, it is possible that the smaller territory size during the incubation and nestling stages was due to the availability of a superabundant food supply at this time (Lack 1950; Perrins 1965, 1970).

There are 2 explanations for the preponderance of whisper songs during incubation: (1) pair bond maintenance, and (2) advertising to rival males. These explanations are not mutually exclusive. With the more stable territorial situation during incubation, a lower intensity territorial song is all that may be required to reassert a territorial holder's presence to his neighbors. The low degree of male-female association supports the pair bond maintenance function of whisper song (Table 2).

On 14 June a predator took the 4 nestlings. The female began building the second nest 15 cm off the ground in juniper shrubbery, 35 m west of the first nest. The new nest was situated between the activity centers of 2 adjacent pairs, in a region that had not been frequently used. The male immediately began establishing his exclusive copulatory rights over the female in the new area. Rates of defensive posturing, chasing per min and singing advertising song increased. It was evident that while the male and female re-established the pair bond, the male's territorial behavior changed considerably in response to the female's behavior.

While the female built her second nest the male remained close to her.

He usually sang or foraged within 15 m of the nest-site, and the foraging areas of both adults decreased. Male and female foraging areas increased during renesting and male rate of singing remained at a moderately high level. As the young dispersed during the fledgling stage territorial boundaries seemed to break down. Breakdown of territorial boundaries during the fledgling stage has been noted in a number of species (e.g., Hinde 1952, Stefanski 1967, Yarrow 1970).

Environmental changes, interactions between conspecifics, and/or seasonal gonadal cycles may lead to many territorial alterations. For this pair of White-throated Sparrows, however, my intensive observations reveal that there were proximate changes in male territorial behavior and in the sizes of activity spaces directly related to the behavior and movements of the female and to the stage of the breeding cycle.

SUMMARY

Through detailed observations I examined the territorial and mate guarding behavior in a mated pair of White-throated Sparrows. I recorded the birds' location and behavior each min for a total of 261 h (male for 197 h and female for 64 h). To obtain replicates within each of the stages of the nesting cycle I divided the data into samples of 100 min. Area was measured by using a bivariate home range model which generated a 95% confidence ellipse around each sample. I found that the female and the stage in the breeding cycle were responsible for the proximate changes in the areas used by the male for foraging and singing, as well as for changes in male territorial behavior (the singing of advertising and whisper song, defensive posture, and chases).

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NEW LIFE MEMBER

Jeffrey A. Spendelow, a graduate student in biology at Yale University, is a new Life Member of the Wilson Society. His doctoral research is on genetic variation in egg white proteins of Red-winged Blackbirds (*Agelaius phoenicius*), although he is interested in avian population biology and ecology as well. He is currently working on a colonial bird nesting project but hopes to work on herons in the future. Mr. Spendelow is an active bird bander and is a member of several professional societies. He is married with one child.