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**Site Tenacity and Dominance
in Wintering White-throated Sparrows *Zonotrichia albicollis*
(Passeriformes: Emberizidae)**

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Abstract

Supplemental feeding of a wintering population of 132 white-throated sparrows was suspended in midwinter to determine characteristics associated with the tendency to remain within previously established home ranges after a drop in food levels. Site-faithful birds tended to be dominant, to have high levels of subcutaneous fat and to reside in certain regions of the study area. The high site fidelity of dominant sparrows reaffirms the importance of dominance in structuring populations.

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Introduction

Many birds form strong attachments to the home ranges they use in winter (NICKEL 1968; RALPH & MEWALDT 1976; but see also SWENSON et al. 1988; BEKOFF & SCOTT 1989). Among nonmigratory species this attachment might allow an individual both to increase its likelihood of surviving and to acquire a breeding territory in the subsequent spring (ARCESE & SMITH 1985; EDEN 1987; NILSSON & SMITH 1988). Migratory birds, too, exhibit strong fidelity to wintering sites. Individuals of a variety of species (including passerines, shorebirds, hawks and cranes) often migrate thousands of km each year to return to the same small winter ranges (SCHWARTZ 1964; NICKELL 1968; SMITH & STILES 1979; MCNEIL 1982; POGSON et al. 1988).

Despite these reports, neither between- nor within-year fidelity to wintering sites has been studied in detail. An examination of individual variability in site tenacity during winter might clarify the conditions under which site tenacity occurs.

This study examined site tenacity within a winter in migratory white-throated sparrows, a species in which individuals maintain close associations with small ranges both within and between winters (PIPER & WILEY 1990 a). White-throated sparrows forage on the ground in hedgerows and brushy areas that provide shelter from predators (SCHNEIDER 1984). The small ranges of individuals (usually less than 0.5 ha; see PIPER & WILEY 1990 a) overlap broadly, and they often feed together in small loose flocks. Recently it has been shown that the dominance status of a white-throated sparrow, as indicated by agonistic interactions at food, tends to decrease as it interacts farther away from the center of its winter range (PIPER & WILEY 1989 a). Perhaps because dominance is site dependent, dominant sparrows tend to use smaller ranges than subordinates (PIPER & WILEY 1990 a).

As a means of studying the variability among individuals in site tenacity, I induced many of the birds in a large marked population to abandon their winter ranges and then examined the correlates of site tenacity by means of a multivariate analysis.

Methods

Study Area and Trapping Regimen

The investigation of site tenacity described here, carried out from Oct. 1985 through Apr. 1986, was part of a study of the behavior of wintering white-throated sparrows conducted at Mason Farm Biological Reserve in Chapel Hill, North Carolina, from 1982—1983 through 1986—1987. The white-throated sparrows used in the experiment constituted part of an annual winter population of about 300 that inhabited a semi-isolated 400-m long stretch of hedgerow consisting mostly of rosebushes (*Rosa multiflora*) and bordered by overgrown and cultivated fields, woods and roads.

White-throated sparrows were captured in 17 six-celled treadle traps baited with millet and placed roughly 25-m apart along the hedgerow. Trapping occurred twice weekly from 29 Oct. 1985 through 10 Jan. 1986 between 08.00 and 12.00 h. Traps were prebaited on the day before trapping so birds could feed at them without capture. Food was also provided at four observation sites on every day from 1 Dec. through 9 Jan., except on 12 Dec. Thus, sparrows in the study area had access to artificial food on 67 of 74 days between 29 Oct. and 10 Jan., including every day from 28 Nov. through 10 Jan. Between feeding at traps and at observation sites, an estimated 2 g of millet was available per bird per day from 29 Oct. through 10 Jan., an amount equal to about 1/3 of the daily requirement at normal winter temperatures (based on findings of CARACO et al. 1990).

To determine locations of winter ranges of white-throated sparrows, I first determined the relative locations of all traps with compass and measuring tape and assigned X, Y coordinates to each trap (PIPER & WILEY 1990 a). The means of coordinates of all trapping locations (weighted according to the number of captures at each location) were then computed for each bird to determine its mean trapping point, an indication of the center of its range (PIPER & WILEY 1989 a). Because most sparrows were seen and trapped consistently within small winter ranges (see PIPER & WILEY 1990 a), even individuals with single captures (26 of 127 or 20 % of the total) were included in the analysis (overall mean number of captures = 4.4 ± 2.6 SD).

Unbanded sparrows caught in traps were given unique combinations of colored leg bands, sexed by laparotomy (see WINGFIELD & FARNER 1976) and assigned to an age class based on skull pneumatization (see PIPER & WILEY 1989 a). In addition, for all birds not previously captured in 1985—1986, length of wing chord (nearest 0.5 mm) and brightness of crown stripes were measured to determine size and morph, respectively (see PIPER & WILEY 1989 b). Finally, sparrows were scored for the amount of subcutaneous fat in the furcular and abdominal regions (PIPER & WILEY 1990 b) and released at the traps where they were captured (usually within 2 h of their time of capture). All birds retrapped in 1985—1986 were immediately scored for fat and released.

Investigation of Site Tenacity

To examine site tenacity during a reduction in food, I suspended feeding at traps and observation sites from 11 Jan. to 16 Mar. and determined local movements of individuals by conducting daily censuses. During each census, I walked along paths adjacent to traps and in outlying regions and recorded positions of color-banded individuals relative to a set of census points with known X, Y coordinates. The amount of time spent censusing each interval of the study area was recorded to ensure even coverage of the study area (mean time spent censusing = 2.4 h per day). Finally, I computed a mean census point (similar to mean trapping point) as an index of each bird's focal point of activity after the suspension of feeding. Birds with single sightings (7 of 127 birds) were included in the analysis (mean number of sightings per bird = 10.3 ± 5.8 SD).

The distance each bird moved, a measure of its site tenacity, was equal to the distance between the coordinates of its mean trapping point from 23 Oct. to 10 Jan. and mean census point from 11 Jan. to 16 Mar. I used a natural logarithm transformation to normalize the distribution of distances moved. Only 14 of 297 residents (5 %) of the study area were not seen at least once after the suspension of feeding. Because it was impossible to determine if these individuals had died or emigrated, they were excluded from the analysis.

After I resumed providing food at traps on 17 Mar., I carried out censuses on 8 more days (for 21 h in all) until 1 Apr. and calculated a mean census point for each bird after the experiment.

Measurement of Dominance

Between 4 Dec. and 10 Jan., I observed dominance interactions among color-banded sparrows at four feeding sites situated at 75-m intervals along the trapline. Although 63 % of all interactions ($n = 8214$) were recorded when birds supplanted each other at artificial food, interactions recorded among birds on the ground and in bushes near the feeding areas revealed that dominance relationships remained consistent in different contexts. I considered one bird dominant to a second if it supplanted that bird in 75 % or more of their interactions (see also PIPER & WILEY 1989 a). For each sparrow that interacted with 10 or more opponents at a single site (mean number of opponents = 30 ± 13 SD, $n = 127$), I calculated a dominance proportion (number of opponents dominated divided by total number of opponents).

The raw dominance proportion computed for each bird tended to underestimate maximum dominating ability because dominance is site dependent: birds observed to interact far from their mean trapping points (where their dominance scores were highest) received dominance scores below their maximum values. To standardize dominance scores with respect to location, I computed the distance between a bird's mean trapping point and the site where it interacted and multiplied this distance by the rate at which dominance proportion decreased with distance away from a bird's mean trapping point (based on a regression equation from data of 1983—1984 and 1984—1985, see PIPER & WILEY 1989 a). I then added this product to each bird's dominance proportion to obtain its corrected dominance proportion, an estimate of its dominance proportion at the center of its winter range. Corrected dominance proportions, which varied between 0 and 1.0, were normalized with the logit transformation (SNEDECOR & COCHRAN 1967).

Measurement of Other Possible Correlates of Site Tenacity

Five potential correlates of site tenacity were determined from measurements previously described or from trapping data. First, I classified each bird as a white or tan morph (LOWTHER 1961) based on its age, sex and the brightness of the median and superciliary stripes in its crown (PIPER & WILEY 1989 b). Second, mean level of subcutaneous fat in the abdominal and furcular areas, an index of ability to survive periods without food (KING 1972), was computed based on fat scores obtained from 15 Dec. to 10 Jan. (PIPER & WILEY 1990 b). Third, fall arrival date was computed by subtracting one-half of the mean number of days between successive captures of a bird from the date it was first trapped (see PIPER & WILEY 1989 a). Fourth, each sparrow was assigned to a residence class to indicate the number of years it had been resident in the study area (PIPER & WILEY 1989 a). Finally, I classified each bird according to the region of the study area that contained its mean trapping point before the suspension of artificial feeding. These regions corresponded to four consecutive sections of the trapline, each of which contained four or five traps and one observation site.

Statistical Analysis

I carried out an analysis of covariance to determine which of the categorical and continuous characteristics measured were correlates of site tenacity. The criterion (dependent) variable in the analysis was distance between mean trapping point during the period when artificial food was provided and mean census point during the period when artificial feeding was suspended. Predictor (independent) variables consisted of two known correlates of dominance, age class and sex (PIPER & WILEY 1989 a), and 8 other characteristics: corrected dominance proportion, morph, brightness of the crown, length of wing chord, mean level of subcutaneous fat from 15 Dec. through 10 Jan., residence class, fall arrival date and region that contained the mean trapping point.

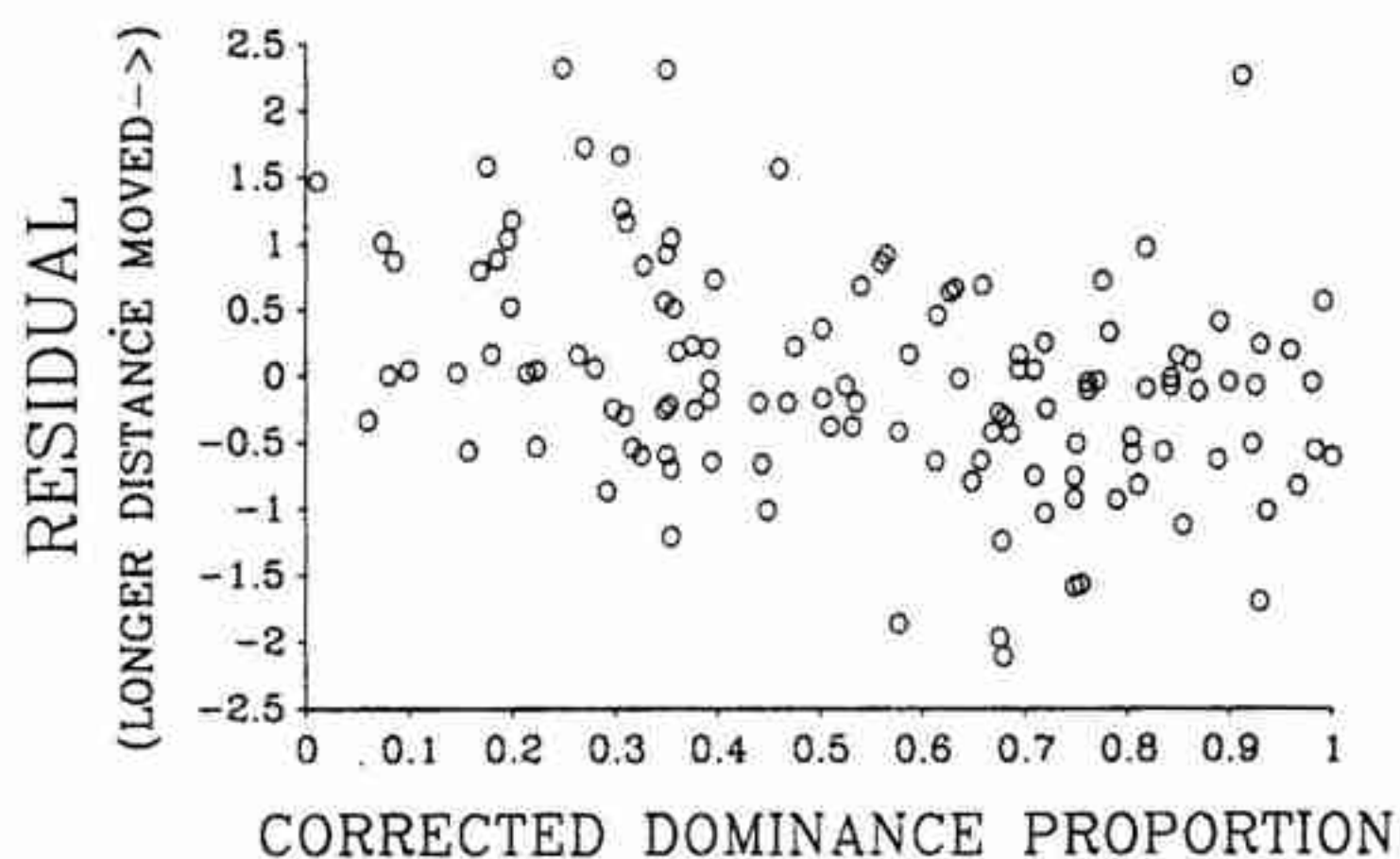
The final model was obtained in three steps. First, I analyzed all predictor variables with stepwise multiple regression (SYSTAT Inc., Evanston) to find those most strongly correlated with site tenacity. Second, I constructed a model consisting of the significant variables from the stepwise process and all their interactions. Third, backward elimination (DRAPER & SMITH 1966) was used to produce a model that contained only significant correlates. A significance level of 0.005 was used because of the large number of variables tested (the modified Bonferroni method, see KEPPEL 1982).

Results

The suspension of artificial feeding along the trapline was followed by widespread emigration from the area along the trapline. Of 173 birds that had been observed regularly along the trapline before 10 Jan., 64 (34 %) were not seen in the area between 11 Jan. and 16 Mar. despite daily censuses.

Although dominance, fat level, region, length of wing chord and residence class were initially selected by the stepwise multiple regression as correlates of site tenacity, only the first three variables satisfied the α level of 0.005. The final model for analysis of covariance revealed that dominant birds ($F_{1,121} = 15.2$, $p < 0.0005$; Fig. 1), those with high fat levels ($F_{1,121} = 15.7$, $p < 0.0005$; Fig. 2) and those in regions 2 and 4 ($F_{3,121} = 4.6$, $p < 0.005$, Fig. 3) tended to remain in the same areas in spite of the removal of supplemental food. The relationship between dominance and site tenacity was striking: 83 % of all birds with high corrected dominance proportions (0.75 to 1.00; $n = 35$) remained within 60 m of their mean trapping points, while only 16 % of the birds with low dominance proportions (0 to 0.25; $n = 19$) did so. R^2 was 0.34, and no interaction was significant.

Fig. 1: Relation between corrected dominance proportions and residuals from the model of site tenacity that included only fat levels and regions of the study area as predictors. The figure indicates that, with other variables controlled, dominant birds moved shorter distances during the suspension of feeding than did subordinates



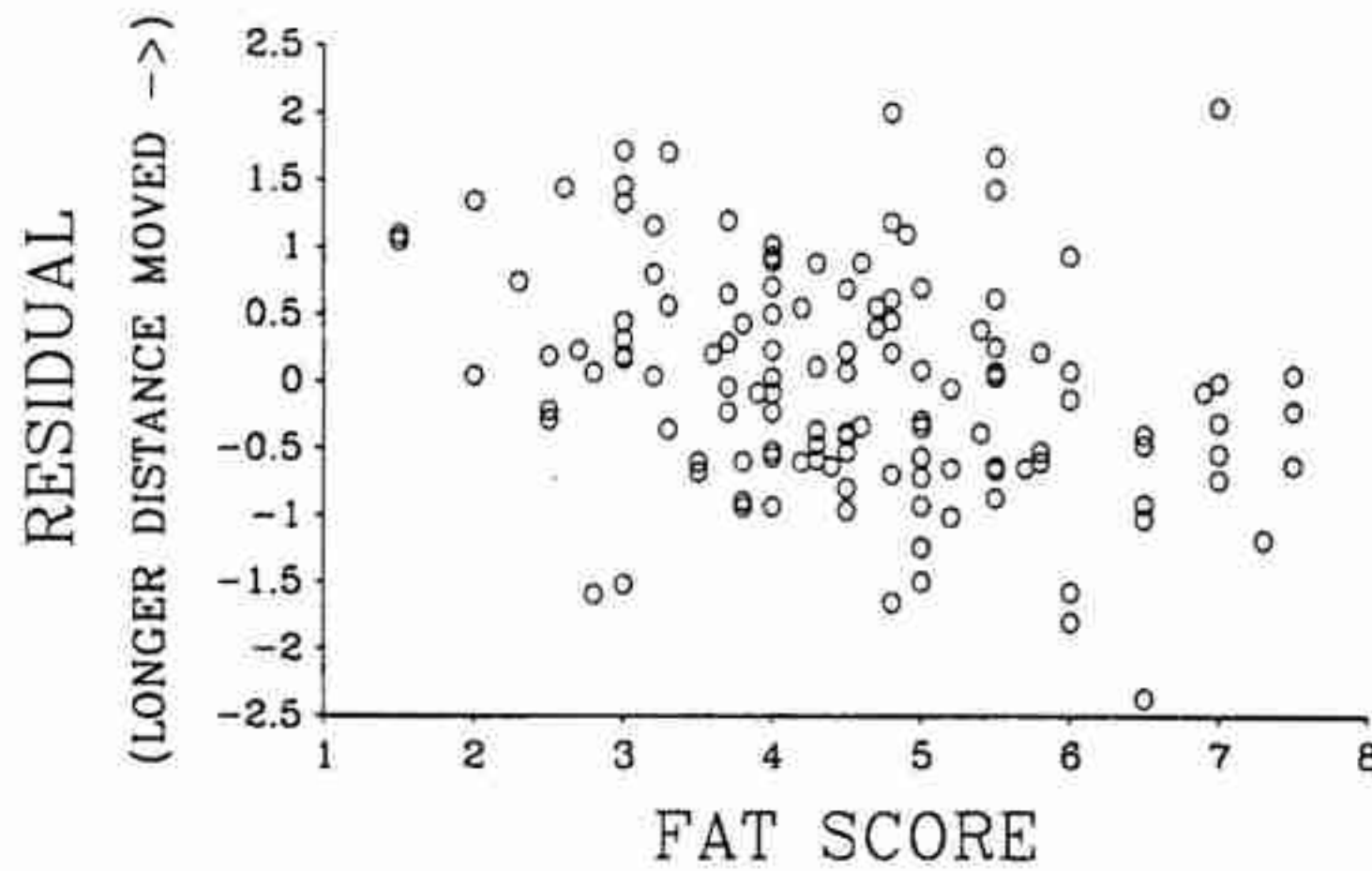


Fig. 2: Relation between fat levels and residuals from the model of site tenacity that included only corrected dominance proportions and region of the study area as predictors. The figure shows that, with other variables controlled, fat birds moved shorter distances during the suspension of feeding than did lean birds

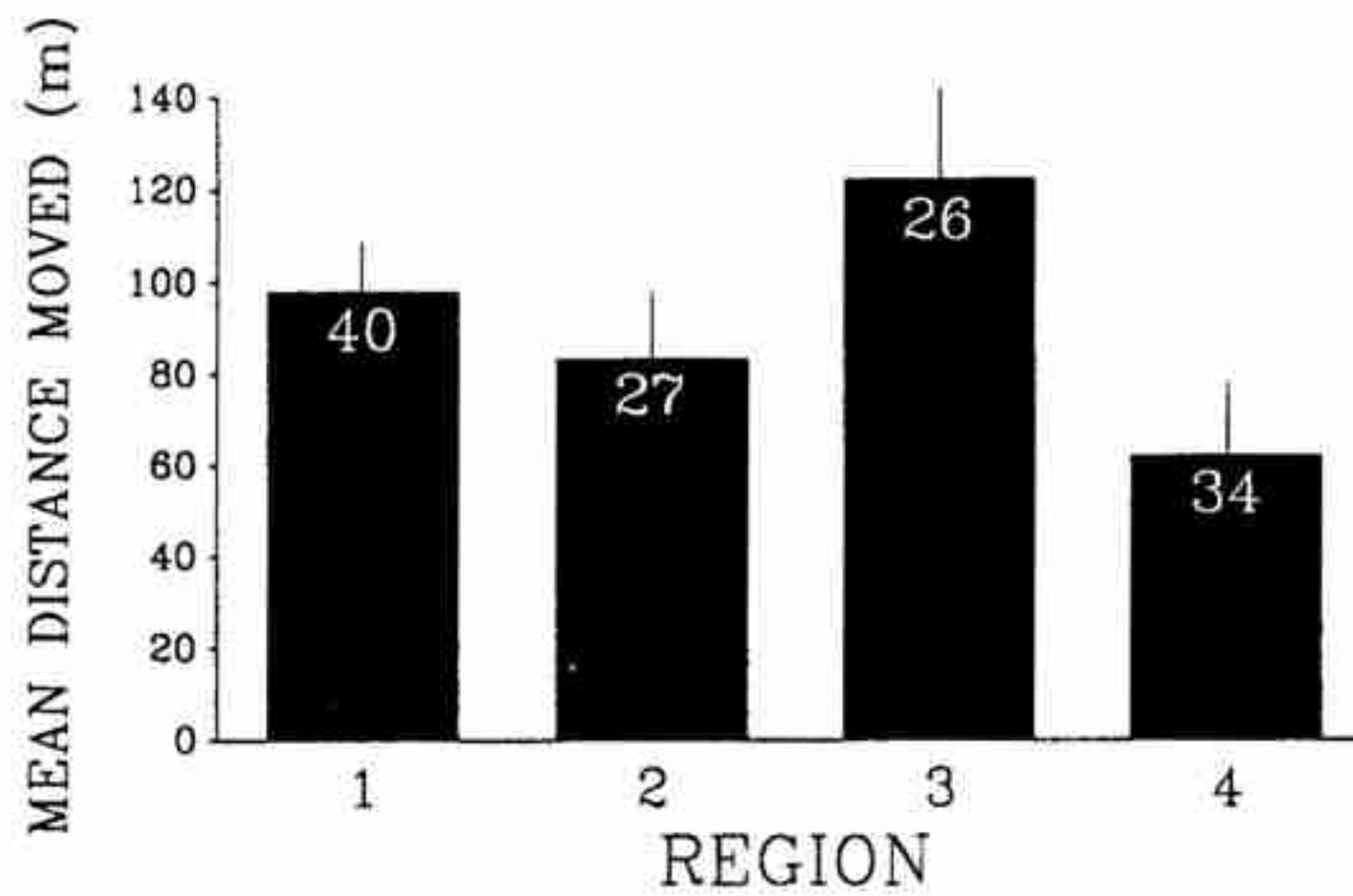


Fig. 3: Means and SE for distances moved by birds in the four regions of the study area

Individuals tended to return to their ranges after trapping and supplemental feeding were resumed on 17 Mar. Of the 96 birds seen on censuses both during the suspension and after trapping was resumed, 70 (73 %) were closer to their mean trapping points during the latter period (Wilcoxon test, $t = 4.5$, $p < 0.001$, two-tailed).

Discussion

Use of Suspension of Feeding to Measure Site Tenacity

Although the suspension of feeding at traps and observation sites during midwinter is not strictly analogous to any natural occurrence, the general problem of a rapidly-changing food supply is one faced by white-throated sparrows. After occasional snowfalls, for example, availability of food is dramatically reduced for a period of up to a week in North Carolina. Although the suspension of feeding lasted for two months, its impact on food was much smaller because it occurred during a winter of low snowfall (3.8 cm total, about 12 cm below average) when natural food remained available. The tendencies of individu-

als to return to their original winter ranges after feeding was resumed strongly suggests that the suspension of feeding, and not some other factor, caused them to abandon their ranges in the first place.

Accuracy of Measurements Based on Trapping and Censuses

The validity of my analysis depended on the accuracy of tracking movements of white-throated sparrows by means of trapping and census data. This task was simplified by the tendencies of individuals to maintain ranges of 0.25 ha or less that were consistent in size and location between winters and by the agreement between maps of individuals' ranges based on trapping and census data (PIPER & WILEY 1990 a). Of the 127 sparrows in this study, 113 (89 %) had more dominance interactions in the region of the trapline where they were trapped most frequently than in any other region, further evidence that a sparrow's trapping record reflected where it spent its time.

That the trapping done to determine the original locations of birds' winter ranges was conducted in a smaller area than were the censuses used to monitor movements after the suspension of feeding created a potential problem: birds whose original winter ranges lay outside the main trapline might have appeared to move after feeding was suspended because of the failure of the trapline to define their original ranges completely. However, occasional censuses and trapping in outlying areas revealed that most white-throated sparrows rarely ventured beyond the trapline when it contained artificial food, in part because the trapline was isolated from other suitable habitat. In a trapping area 150-m distant from the main trapline, for example, only 5 of 135 captures of white-throated sparrows between 29 Oct. and 10 Jan. were of birds from the main trapline. Thus, most of the activities of birds in the study were confined to the main trapline.

As a final safeguard against the possibility that the apparent movements reported here resulted simply from the different distributions of trapping and census points, I carried out an additional analysis identical to the first except that I used a dichotomous (distance moved ≥ 60 m or < 60 m) rather than a continuous criterion variable. In light of the small ranges of white-throated sparrows (see PIPER & WILEY 1990 a), individuals that moved 60 m or more were almost certain to have abandoned their ranges. Hence, the dichotomous criterion variable permitted a conservative test of site tenacity. The result was similar to that of the main analysis ($p < 0.0005$ for dominance and fat level; $p = 0.007$ for region). I conclude that the differences in distributions of trap locations and census points did not bias the conclusions.

Fat Levels and Site Tenacity

The correlation of site tenacity with level of subcutaneous fat suggests that a bird's condition affects the strength of its attachment to a winter range. Because fat deposits are a means by which ground-feeding birds avoid starvation after snowfalls (KING 1972; KETTERSON & KING 1977; ROGERS 1987), it makes sense that individuals with low fat levels should abandon their ranges readily to seek food elsewhere. Indeed, an individual that has been able to store little fat in one area

might be able to increase its fat storage elsewhere, because levels of natural food apparently vary from one small area to another (PIPER & WILEY 1990 b).

Region and Site Tenacity

The weak tendency for birds in regions 2 and 4 to have high site tenacity probably resulted from the locations of new areas to which birds immigrated as well as the characteristics of the original regions. For example, many sparrows from all regions used areas in and around region 4 during the suspension of feeding. The proximity of this region to their original ranges caused birds in region 4 to appear to be relatively site faithful.

The relationship between region and site tenacity shows that a bird's choice of a winter range is important because individuals settling in ranges that have high food levels in midwinter can remain within the ranges they establish in early winter and supplant immigrants at food. The low site tenacity of many white-throated sparrows in midwinter might result from an inability to predict food levels during midwinter based on food levels at their times of arrival, a problem complicated by the apparent variability in food levels between years (PULLIAM & ENDERS 1971).

Dominance and Site Tenacity

Since dominant birds have higher fat levels than subordinates in white-throated sparrows (PIPER & WILEY 1990 b), one might conclude that the strong correlation between dominance and site tenacity resulted from a tendency for dominants to remain in their ranges because of their easy access to food (PIPER 1990) and consequent high fat levels (PIPER & WILEY 1990 b). Had this been the case, however, dominance and fat level would not both have produced distinct partial correlations with site-tenacity. The results presented here suggest that some aspect of dominance itself, apart from its relationship with fat level, was related to the tendency to be site faithful. The tendency of dominant white-throated sparrows to remain in their winter ranges despite a drop in food levels supports the view that dominant birds remain in their ranges to exploit the advantage of their dominance there (PIPER & WILEY 1989 a).

Based on this and other recent findings, it is possible to obtain a general picture of the importance of dominance to the winter ecology of white-throated sparrows. Dominant birds, who tend to be old males (PIPER & WILEY 1989 a), remain within small ranges where they can maintain high fat levels (PIPER & WILEY 1990 a, b), perhaps by usurping food from subordinates. They apparently resist moving because, in abandoning familiar areas, they become subordinates (because dominance is site-dependent). When food levels drop in their ranges, dominants face a tradeoff: they can remain in their ranges and supplant what few subordinates remain there, or they can abandon their ranges and try to locate food elsewhere. Apparently the advantages of remaining dominant are sufficiently great that dominants rarely move. In contrast, subordinate birds, who are often young females (PIPER & WILEY 1989 a), normally use larger areas in foraging (PIPER & WILEY 1990 a). If food becomes scarce in their winter ranges, subordi-

nates readily abandon them and search elsewhere because, unlike dominants, their ability to usurp food from conspecifics varies little from place to place (PIPER & WILEY 1989 a). Although the nomadic existence of subordinate birds might allow them to determine food levels in different areas and settle where supplies are highest, this pattern of behavior has two drawbacks. First, birds outside their usual ranges must avoid the attacks of established residents, who tend to attack and fight with intruders (BALPH 1977; WATT 1986; PIPER & WILEY, unpubl. data). Second, birds that wander widely are inevitably less familiar with their large ranges than are more sedentary individuals and thus are probably less familiar with roost sites and routes of escape that can be used when predators attack.

The link between social dominance and local movements seems likely to occur in other species, but care must be taken to avoid confusing dominance itself with other correlated factors such as age, sex and condition. In a species where males and old individuals tend to be dominant, high rates of emigration among females and young animals (e. g. LUNDBERG 1985) suggests, but does not demonstrate, that dominance itself influences emigration.

Despite the difficulty of showing a relationship between winter movements and dominance per se, there is abundant indirect evidence for such a relationship in birds (see also GAUTHREAU 1978). In many avian species, young birds and/or females, who tend to be subordinate, often abandon good habitats, leaving a disproportionate number of old birds and/or males there (SMITH 1984; ARCESE & SMITH 1985; LUNDBERG 1985; RABENOLD & RABENOLD 1985). Moreover, among captive dark-eyed juncos (*Junco hyemalis*), subordinates faced with competition for limited food during midwinter showed nocturnal restlessness indicating a tendency to migrate (TERRILL 1987). Further study of other species is needed to determine if the relationship between dominance and site-fidelity is widespread.

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