

Correlates of range size in wintering white-throated sparrows, *Zonotrichia albicollis*

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Abstract. A 400-m trapline along a hedgerow was used to calculate sizes of winter ranges in a migratory population of 328 white-throated sparrows during three winters. Although range size varied greatly among individuals, the ranges of most sparrows extended for 100 m or less along the trapline. Birds tended to return to the same location and to have ranges of similar sizes from year to year. A multivariate analysis of variables affecting range size revealed that dominant birds tended to have small ranges, possibly because their dominating ability would decrease if they left familiar areas. Range size also decreased with age, an apparent indication that old and young individuals used space differently in attempting to survive a winter.

A large body of literature describes the use of space by animals. Activity ranges of many species of mammals and large birds (reviewed by Waser & Wiley 1980) have been determined through simple observation (Struhsaker 1975), by radio-telemetry (Heisterberg et al. 1984) or by live-trapping (Desy et al. 1989). In addition, the restricted movements of some breeding birds have made it feasible to construct territorial maps, and a number of studies have compared sizes of territories of different individuals or species (Knapton & Krebs 1974; Myers et al. 1979).

Activity ranges are poorly known for other groups such as wintering passerine birds (but see Schwartz 1964; Catterall et al. 1989). However, the tendency of individual passerines to migrate year after year to specific wintering locations (e.g. Mewaldt 1976) suggests that activity ranges might have great ecological importance in this group.

As a means of investigating the use of space in a small passerine, we measured range size, determined its constancy between years, and examined its correlates in a wintering population of white-throated sparrows. Most individuals of this species migrate hundreds of kilometres annually between a specific wintering site in the southeastern United States and their breeding grounds in the northeastern United States or Canada.

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METHODS

Trapping Regimen and Measurement of Range Size

We used trapping data to determine winter ranges in a marked population of white-throated sparrows in 1983–1984, 1984–1985 and 1986–1987 at Mason Farm Biological Reserve in Chapel Hill, North Carolina. Trapping was carried out two to three times weekly at 17 stations spaced at roughly 25-m intervals along a linear hedgerow bordered by fields (Fig. 1). Each station consisted of a six-celled treadle trap baited with millet and placed 1 m above ground on a wooden platform. Sparrows captured previously were scored for level of subcutaneous fat and released immediately. Unbanded white-throated sparrows were carried to a field station and given unique combinations of coloured leg bands. The following measurements were made on each bird: extent of skull pneumatization (Wiley & Piper, in press), length of unflattened wing chord (nearest 0.5 mm), amount of subcutaneous fat (Piper & Wiley, in press a) and brightness of crown stripes (Piper & Wiley 1989a). Sex was determined for each bird by laparotomy (see Piper & Wiley, in press b). After inspection and measurement, each sparrow was released at the trap where it had been captured, usually within 1.5 h of initial capture. Our procedures had no detectable effects on local movements or condition (see also Piper & Wiley, in press b).

Distances and directions between trap locations were determined with compass and measuring tape, and each location was assigned *X* (north–south)

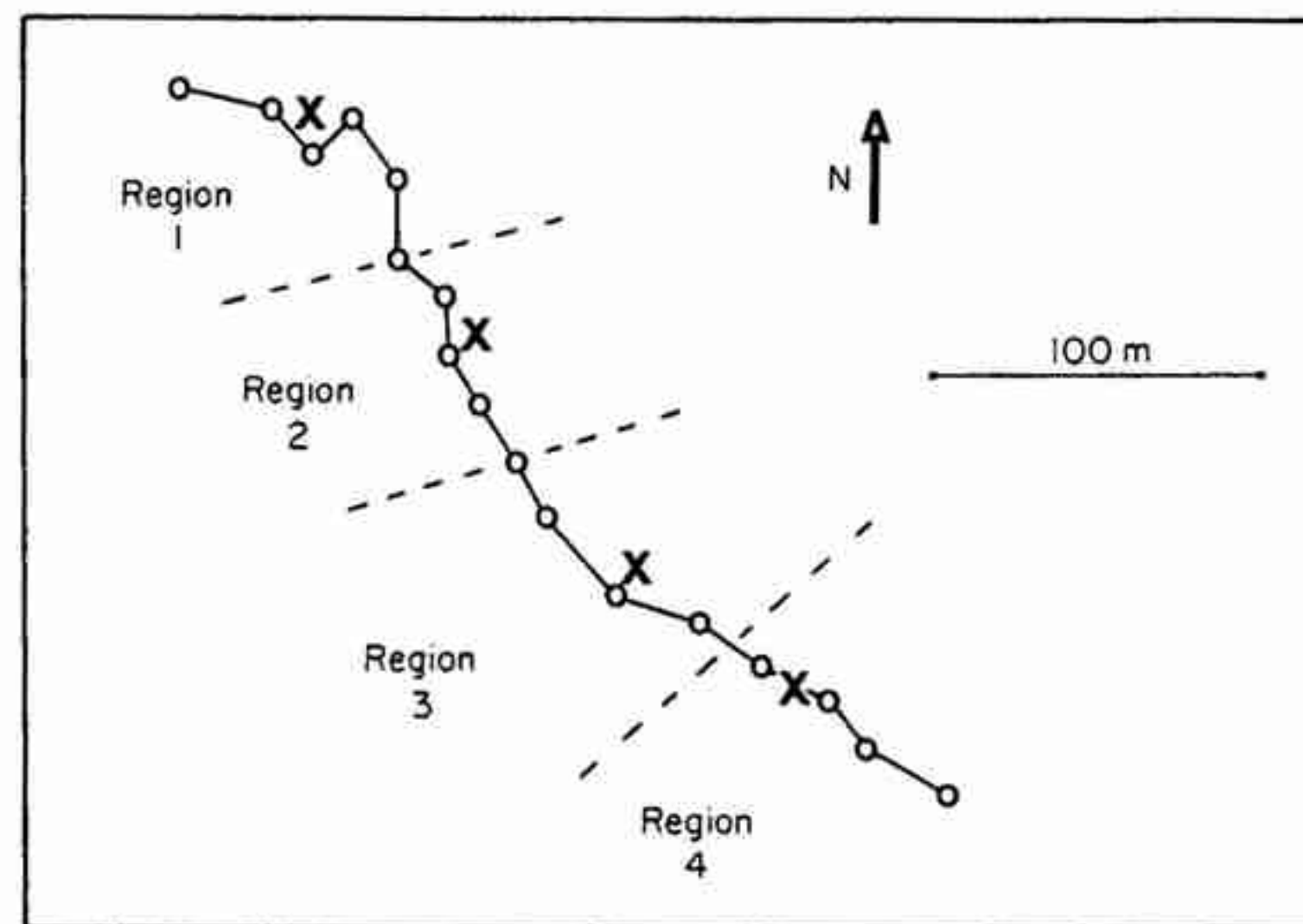


Figure 1. Map of the study area showing the trapline and sites with artificial food. ○: trap; X: observation site.

and *Y* (east–west) coordinates. Since the birds spent most of their time on or near the ground during the winter, we disregarded the height of the habitat. A mean trapping point, used to indicate the centre of a bird's range, was computed for each individual by taking the mean of the *X* and *Y* coordinates for all of its trapping locations in a winter.

Preliminary investigation revealed that white-throated sparrows usually stayed within small ranges and varied greatly in the number of times they were captured. Therefore, to avoid bias by the number of observations, we used the univariate normal approximation to measure each bird's range size (see Jennrich & Turner 1969). Range size, computed only for individuals with three or more captures, was taken as the standard deviation for the locations of all of a bird's captures multiplied by two (because individuals were captured in two directions along the trapline relative to their mean trapping points). We took the natural logarithm of range size to normalize it. Nine birds captured in only single locations and initially assigned range sizes of 0 were omitted because we decided that their ranges had not been adequately defined by our techniques. Exclusion of these individuals did not alter the results.

Measurement of Potential Correlates of Range Size

We measured dominance of individual sparrows by observing interactions at four feeding sites along the trapline during three mornings each week (Fig. 1). A bird that exhibited dominance over a given opponent in 75% or more of the total interactions

between the two birds was considered the dominant bird of that pair. A small number of dyads in which neither bird dominated the other in at least 75% of the total interactions were viewed as undefined and excluded from the analysis (see Piper & Wiley 1989b). Dominance proportion, which we used as an index of dominance, was the number of opponents a bird dominated divided by the number of opponents with which it interacted; the value was then normalized with the logit transformation (Snedecor & Cochran 1967). Sparrows that interacted with fewer than 10 opponents were excluded from the analysis ($\bar{X} \pm \text{SE}$ number of opponents = 55.5 ± 1.4 , $N = 328$).

Nine potential correlates of range size (in addition to dominance, sex and length of wing chord, see above) were determined as follows (see also Piper & Wiley 1989b): (1) age-class, by means of skull pneumatization in the winter of a bird's initial capture; (2) crown brightness, by adding both observers' brightness scores for the median, lateral and superciliary stripes; (3) morph (white or tan), by applying a simple formula to the scores for its median and lateral stripes (Formula 1 from Piper & Wiley 1989a); (4) mean level of subcutaneous fat during January and February (an indication of a bird's ability to survive periods of cold weather and snow cover; Piper & Wiley, in press a); (5) residence-class, by counting the number of winters a bird had resided in the study area; (6) arrival date, by subtracting half of a bird's mean trapping interval (mean number of days between captures) from the date on which it was first observed; (7) region of the study area, based on which of four such regions

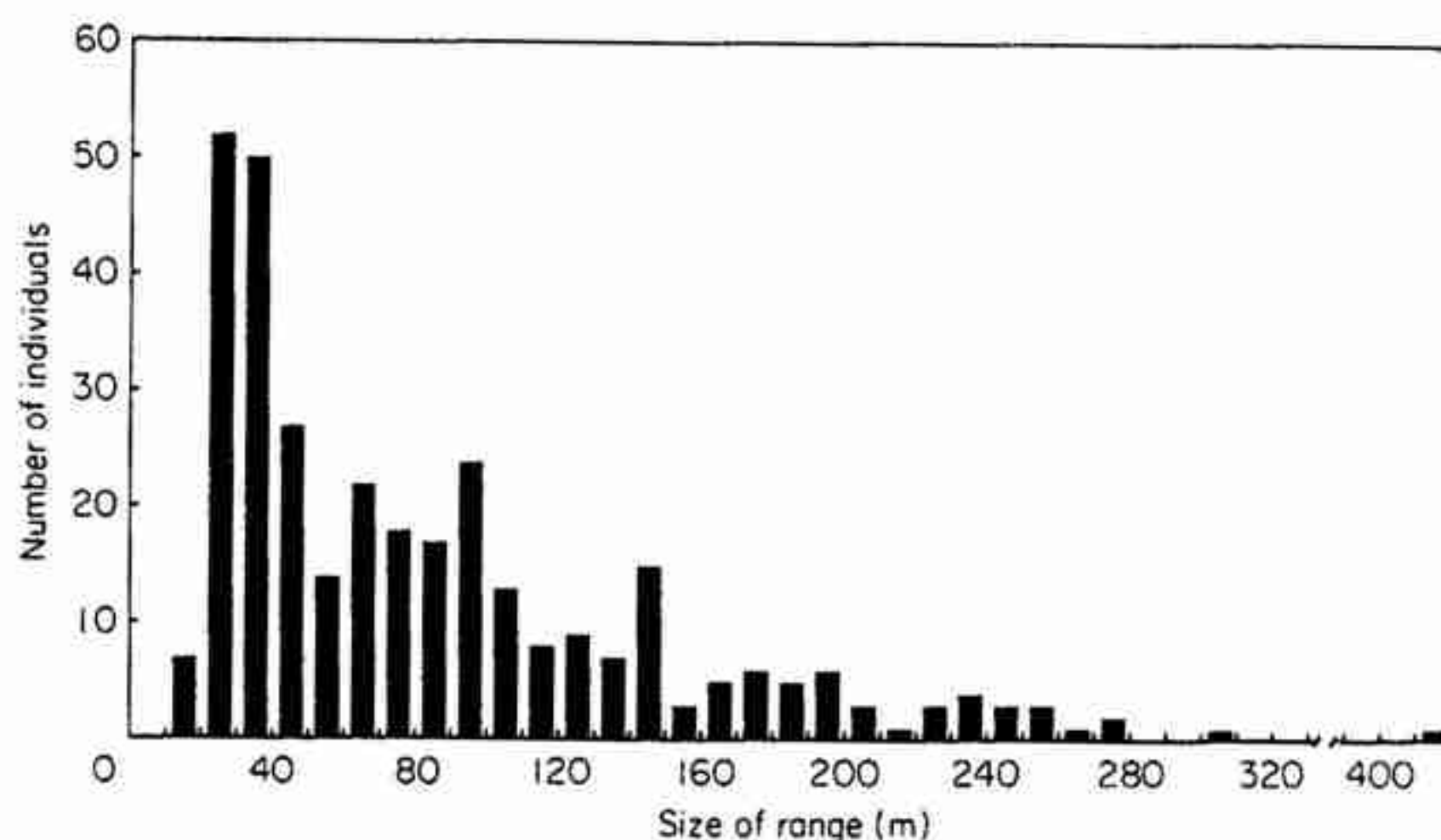


Figure 2. Distribution of range sizes measured as twice the SD of locations along the trapline ($N=328$).

contained its mean trapping point (see Fig. 1); (8) year in which range size was measured (1983–1984, 1984–1985 or 1986–1987); and (9) number of captures (an indication of the frequency with which it visited traps).

Analysis of Factors Correlated with Range Size

Because the potential correlates of range size were both continuous (e.g. arrival date) and categorical (e.g. age-class, sex), we carried out an analysis of covariance (SYSTAT, Evanston, Illinois). The criterion (dependent) variable was range size, while predictor (independent) variables were dominance, sex, length of wing chord (an index of size), age-class, crown brightness, morph, mean fat level, residence-class, arrival date, region, year and number of times captured. To select the strongest correlates, we screened all predictor variables by means of a stepwise multiple regression (SYSTAT), created a model that included all selected variables and their interactions, and used backwards elimination to produce the final model (Draper & Smith 1966). The α level was reduced from 0.05 to 0.004 because of the large number of variables tested (the modified Bonferroni method, see Keppel 1982).

Comparison of Range Size between Years

Sparrows whose range sizes were known in both 1983–1984 and 1984–1985 were used to determine the constancy of range size between years. Range size in 1984–1985 was used as the criterion variable in this second analysis of covariance. As potential correlates, we considered those variables selected as correlates of range size in the main analysis (see

above) and, in addition, range size in 1983–1984. Backwards elimination was then used to remove variables for which α was greater than 0.004.

RESULTS

The computed sizes of white-throated sparrows' ranges varied from 16 to 420 m ($\bar{X} \pm SE = 85 \pm 3$ m, $N=328$); the distribution of range sizes was positively skewed (median = 66 m; see Fig. 2).

Individuals that were dominant ($F_{1,320} = 52$, $P < 0.0005$, Fig. 3) and old ($F_{1,320} = 32$, $P < 0.0005$, Table I) tended to have small ranges. Range size also varied between regions of the trapline ($F_{3,320} = 13$, $P < 0.0005$). Sparrows in regions 1 ($\bar{X} \pm SE = 61 \pm 4$ m, $N=95$) and 2 (71 ± 5 m, $N=77$) had range sizes smaller than birds in regions 3 (103 ± 7 m, $N=81$) and 4 (110 ± 9 m, $N=75$). Finally, range size differed between years ($F_{2,320} = 6.7$, $P < 0.004$). Ranges tended to be larger in 1984–1985 ($\bar{X} \pm SE = 99 \pm 6$ m, $N=131$) and 1983–1984 (81 ± 6 m, $N=68$) than in 1986–1987 (73 ± 5 m, $N=129$). Sex, wing chord length, crown brightness, morph, mean fat level, residence-class, arrival date and number of captures were not related to range size. No interaction term was significant ($R^2 = 0.40$, $N=328$).

The analysis was complicated by a close correlation between age- and residence-class (r^2 between age and residence = 0.77, $P < 0.0005$, $N=328$). To determine whether age- or residence-class was the stronger correlate of range size, we examined correlations between age and range size within the largest residence-class (first-year residents) and

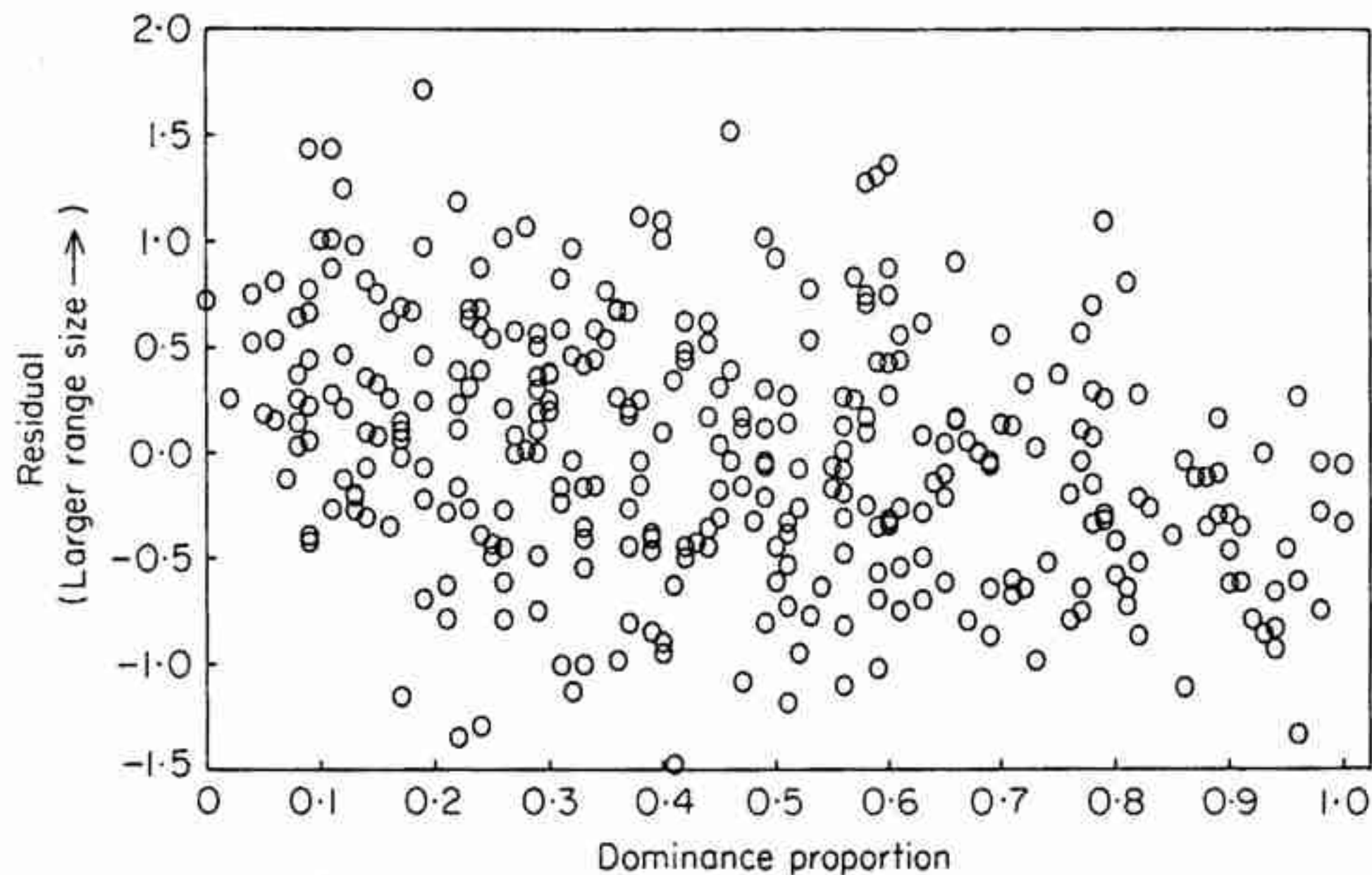


Figure 3. Relation between dominance proportions and residuals from the model of range size that included only age-class, region and year as predictors. The figure shows the correlation between dominance and range size after the effects of age-class, region and year are removed.

Table I. Residuals from the analysis of effects of age on range size and observed range sizes for different ages ($\bar{X} \pm \text{SE}$)

	Age class (winter of life)			
	1 ($N=134$)	2 ($N=117$)	3 ($N=61$)	4 and 5 ($N=16$)
Observed range size (m)*	112 ± 6	73 ± 5	60 ± 6	40 ± 10
Residual†	0.18 ± 0.04	-0.08 ± 0.06	-0.12 ± 0.07	-0.40 ± 0.18

*Observed range sizes (twice the SD of locations along the trapline) reported here do not account for the effects of dominance, region and year.

†Residuals represent values of range size that have been adjusted to account for the effects of dominance, region and year. Thus, these values illustrate the effect of age alone on range size. Comparison of the residuals with the observed range sizes reveals that age alone (when isolated from its correlate, dominance) continued to be correlated with range size beyond the third winter.

between residence and range size within the largest possible age-class (second-winter birds). A weak correlation with age persisted ($F_{1,173} = 5.6$, $N = 181$, $P = 0.02$) under these conditions, while the correlation between residence and range size was absent ($F_{1,109} = 1.1$, $N = 117$, $P = 0.29$). Thus, age appeared to be the stronger correlate.

The size of a bird's range in 1984–1985 was correlated with both the size of its range in 1983–1984 ($F_{1,61} = 20$, $P < 0.0005$) and the region where its

range was located ($F_{3,61} = 6.7$, $P < 0.004$). R^2 for the model was 0.37, and again no interaction term was significant.

White-throated sparrows tended to be observed in the same areas from year to year. Of the 70 individuals captured at least three times in both 1983–1984 and 1984–1985, 63% had mean trapping points in the 2 years less than 20 m apart (Fig. 4). The mean distance moved between years ($\pm \text{SE}$) was 26 ± 3.9 m ($N = 70$).

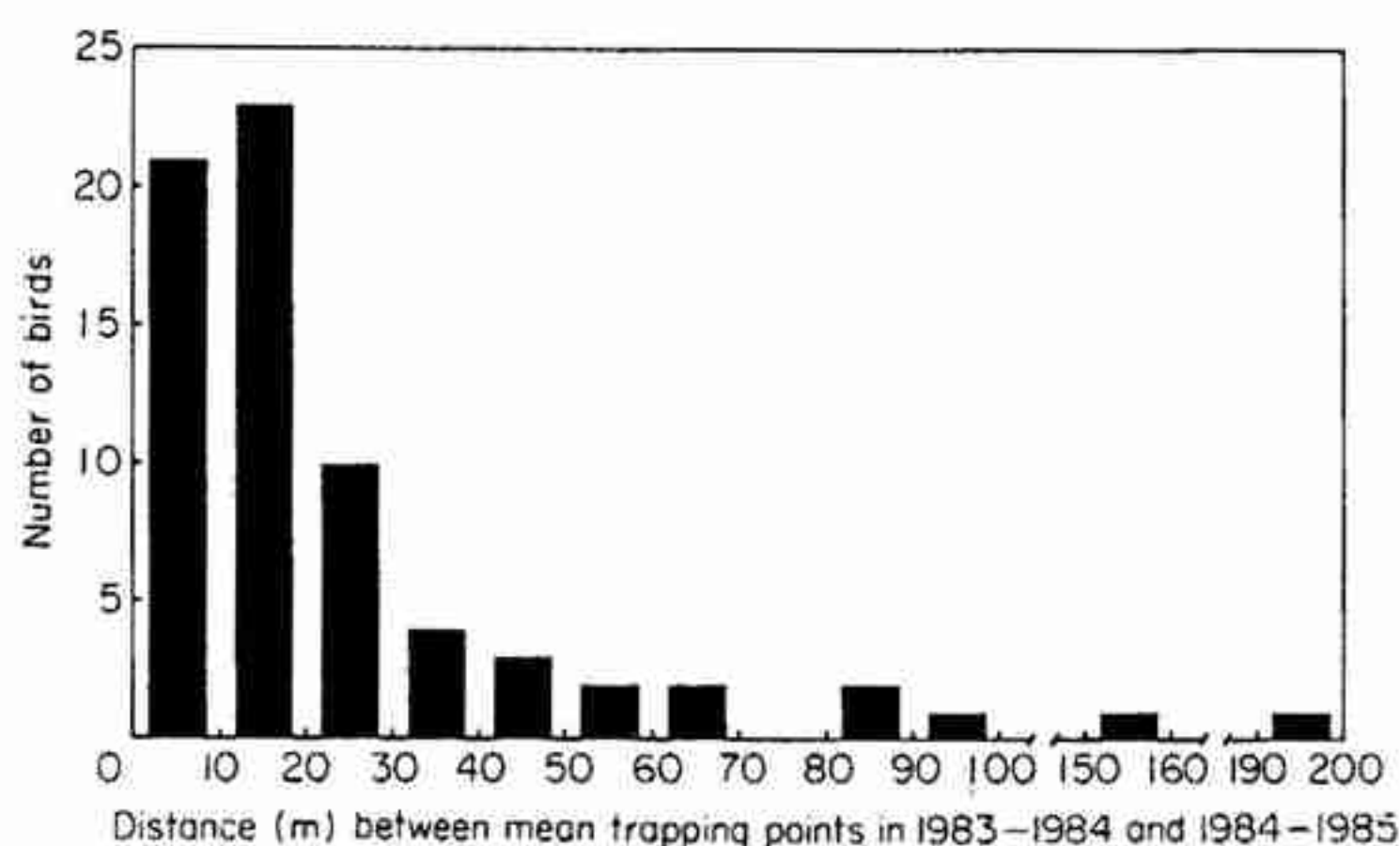


Figure 4. Distribution of the distances between mean trapping points in 1983–1984 and 1984–1985 ($N=70$). The figure shows how far the centres of the ranges of the birds shifted between the 2 years.

DISCUSSION

Measurement of Range Size

We assumed that artificial feeding of the sparrows did not affect their movement patterns substantially. Because food was present only during short periods and was not available on all days, it is clear that individuals had to rely mainly on natural food. Moreover, range size was not correlated with number of captures, an indication that use of artificial food did not strongly affect local movements. However, range sizes computed from captures during normal feeding in the winter of 1985–1986 ($\bar{X} \pm SE = 140 \pm 11$ m, $N=161$) were 19% smaller than those computed from census data during a period in the same winter when feeding was suspended (172 ± 6 m, $N=240$). Although these measures are not strictly comparable, it seems possible that the availability of artificial food caused range size to shrink slightly.

A further question is whether trapping data gave a satisfactory indication of an animal's movements. Range sizes of mammals computed from trapping data typically underestimate values from radio-tracking (Desy et al. 1989). An assumption when using traps to determine ranges is that an animal is equally likely to be caught for a given time spent in any part of its range. Clearly one limitation is that traps only indicate an animal's locations when feeding. Ranges might differ during other activities. However, occasional censuses and casual observations indicated that white-throated sparrows were observed and captured in the same areas. Also, because the primary feature of the habitat sampled by our trapline was a linear hedgerow,

trapping records in this case would provide a geometrically realistic indication of where a sparrow spent its time while feeding.

Although there has been considerable debate concerning the best means of measuring range size in general (see Waser & Wiley 1980), the univariate normal approximation appeared to fit our data well. White-throated sparrows tended to focus their activity about fixed central points, and the probability of them using an area declined away from this central point.

Because we measured range sizes only for birds that resided in the study area for 60 days or more, transients were excluded. It is difficult to estimate how large this segment of the population was because unbanded birds captured in midwinter comprised both transients and birds whose ranges barely overlapped the trapline. However, even assuming that all unbanded birds captured on or after 1 February were transients, this group constituted only 16% of the population ($N=419$, data from 1984–1985).

The Significance of Range Size

We can use our measure of range size to obtain a rough estimate of the total area used by a foraging bird. One standard deviation of trapping locations on either side of the mean should encompass about 68% of the distribution of a bird's foraging time along the hedgerow. Since the hedgerow averaged 2–5 m in width and the sparrows rarely moved more than 10 m from the hedgerow while feeding, the total width of a bird's range perpendicular to the trapline was roughly 25 m. Thus, the approximate area of a bird's range equals our measure of its

range size as a distance along the hedgerow multiplied by 25 m. For instance, first-winter birds spent most of their time in an area averaging 112×25 m, or 0.26 ha. Birds aged 4 years and older used an area averaging roughly 0.10 ha.

The measurements of range size reported here show that a typical white-throated sparrow spends most of the winter within a small range. Ranges of comparable size have been reported for silvereyes, *Zosterops lateralis*, in Australia (Catterall et al. 1989). In some other wintering passerines, like dark-eyed juncos, *Junco hyemalis* (Ketterson & Nolan 1982), ranges appear to be much larger.

An association with a small wintering range probably provides several benefits: (1) permitting a bird to become familiar with and to remember locations of food (Zach & Falls 1976); (2) reducing numbers of attacks from conspecifics because of a bird's tendency to associate with a small number of familiar individuals (Balph 1977); (3) increasing the ability to dominate conspecifics (Piper & Wiley 1989b); and (4) permitting a bird to locate and remember escape routes from feeding areas to be used when predators attack. If it is an advantage to have a small range, then range size might reflect the difficulty that a bird has locating food or satisfying some other basic requirement.

Correlates of Range Size

Dominance

The small ranges of dominant birds apparently was not the result of their having higher fat levels and thus being in better condition than subordinates (Piper & Wiley, in press a). Had this been the case, subcutaneous fat level should have been a stronger correlate of range size than dominance.

Dominant birds might have had smaller ranges than subordinates because the former could remain in the vicinity of sources of artificial food, while the latter had to wander widely in search of natural food. This possibility cannot explain the correlation, though, because range size was correlated with dominance during a period in 1985–1986 when no food was offered and only censuses were used to measure ranges ($r = -0.35$, $P < 0.0005$, $N = 160$).

Instead, the correlation between range size and dominance appears to indicate that dominance itself caused a bird to have a small range. This interpretation is supported by the tendencies of dominant birds to remain within their ranges and of subordinates to abandon them when food levels

drop (Piper 1987). Indeed, two birds, one that maintains a large range and a second that abandons its range altogether, experience similar social consequences. Both dominate relatively few conspecifics, because dominating ability declines rapidly as a bird moves away from a small focal area (Piper & Wiley 1989b). Such site-dependent dominance makes it advantageous for dominant birds to restrict their foraging to small areas in which they can supplant other birds to obtain food and feed without interruption (Caraco 1979). In contrast, subordinates, which lose relatively little dominating ability when they leave their focal areas (because they have little to start with), have little to lose in using larger ranges.

Age

The tendency of old birds to have smaller ranges than young birds is independent of the effect of dominance on range size, as indicated by the analysis of covariance (see also Table I). Thus, as a sparrow becomes older, its winter range contracts regardless of its dominance status.

Although old white-throated sparrows are known to differ behaviourally from young birds in cautiousness while feeding (Piper, in press) and in dominance (Piper & Wiley 1989b), the strong inverse correlation between age and range size, with dominance controlled, has no clear explanation. One possibility is that foraging skills improve as a bird matures, so that it can survive within progressively smaller ranges. A second possibility is that old and young birds have different, but equally successful, strategies to survive a winter. Perhaps young sparrows use large areas where their overall ability to dominate conspecifics is low but their likelihood of finding food is high. Old birds, in contrast, might focus on small areas where their dominance is high but there is some risk of not locating food.

Region

Although it is possible that sparrows actually had ranges of different sizes in different regions of the study area, the correlation between range size and region probably resulted mainly from the differences in the relationship between our trapline and the sparrows' habitat. In regions 3 and 4, the trapline followed a hedgerow beside a narrow road, while in regions 1 and 2, shrubs and woodland edge provided more habitat at a distance from the hedgerow. Thus, to encompass the same area of shrubs, a

range would have to extend along our trapline a somewhat greater distance in regions 3 and 4. By including in our analysis a variable to indicate region of the trapline, we reduced the amount of unexplained variance and increased our ability to define other correlates.

Year

The reason for the differences in range size between years is unclear, though they might have resulted from yearly fluctuations in the availability of natural food, or in the severity of the weather. The intensity of trapping might also have influenced range size ($N=3422$, 4654 and 1996 captures in 1984–1985, 1983–1984 and 1986–1987, respectively).

Range size in a previous winter

Birds present in both years tended to have similar range sizes in 1983–1984 and 1984–1985. This result was clearly seen for a few individuals that wandered widely along the trapline in both winters. It is not likely that the constancy in range size resulted solely from the constancy in dominance (Piper & Wiley 1989b) between years. Had this been the case, dominance would have been a stronger correlate of range size in 1984–1985 than was range size in 1983–1984.

The constancy in range size between years might result from an intrinsic tendency of each sparrow to use space in a particular way. A second possibility is that constant features in a bird's range (like the distribution of hedgerows) might produce similar patterns of movement in different years.

Sparrows also form strong attachments with their winter ranges, so that the locations of ranges change little from year to year (Fig. 4). Philopatry of this kind probably results in a bird using its range more efficiently in later years and thus contributes to the increased condition, as indicated by fat reserves, of prior residents (Piper & Wiley, in press a).

The patterns in range size reported here suggest that a bird's use of space is a basic feature of its behavioural ecology in winter. The sizes of the ranges of individual white-throated sparrows which are consistent between winters, age-dependent and strongly affected by site-dependent dominance, yield useful insights concerning their abilities to survive during winter.

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