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Correlates of dominance in wintering white-throated sparrows: age, sex and location

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Abstract. Correlates of dominance were investigated in a wintering population of white-throated sparrows, *Zonotrichia albicollis*, in 3 successive years at four locations along a 400-m hedgerow. Multiple regression analyses were used to detect characteristics correlated with a sparrow's ability to dominate conspecifics. Age, but not length of time resident in an area, and sex, but not size, both affected dominance. Individuals had higher dominance near the centres of their ranges, and dominance in a bird's first winter was related to dominance in later winters. The presence of site-dependent dominance in this species shows that dominance relations observed at any one location resulted from overlapping dominance fields of the individuals occurring there.

Social dominance can be defined as the ability of one animal to gain priority over another in access to resources such as food or mates (Wittenberger 1981). Many species of wintering passerines form simple dominance hierarchies in winter. Wintering emberizines (Emberizidae) and tits (Paridae), for example, form dominance relationships that are unilateral and stable over long periods of time (Hamerstrom 1942; Sabine 1949; Glase 1973; Rohwer 1977; Balph 1979; Ketterson 1979a; Watt et al. 1984; Hogstad 1987).

One means of understanding the evolution of social dominance is to examine the factors that affect a bird's ability to dominate conspecifics. Numerous studies have described correlates of dominance in passerines (Sabine 1959; Fretwell 1969; Glase 1973; Ketterson 1979a; Parsons & Baptista 1980; Watt et al. 1984; Arcese & Smith 1985). However, three problems hamper these studies. First, most studies examine inherent attributes, such as size and sex (Sabine 1959; Stewart & Darling 1972; Baker & Fox 1978; Watt et al. 1984), but not situational factors like the location of dominance interactions or precedence in arrival on wintering grounds. No study has considered how dominance in emberizines varies with a bird's location, although location does affect winter dominance in permanently resident species of corvids (Brown 1963; Eden 1987) and tits (Glase 1973). Few studies have examined the effects on dominance of hatching date or arrival date on wintering grounds (but see Sabine 1959; Kikkawa 1980; Arcese & Smith 1985). Second, most studies of dominance compare only two age-classes, first-winter and older birds. A number of studies have reported an effect of age on dominance (Glase 1973; Kikkawa 1980; Parsons & Baptista 1980; Arcese & Smith 1985) but have not examined in detail how dominance changes throughout a bird's life. Third, studies of the correlates of dominance rank in emberizines typically suffer from small sample sizes, which prohibit the use of multivariate analyses. In birds there are often strong correlations among factors that could affect dominance: sex with size, age with duration of residency, and, in species that exhibit age- and sex-related plumage variability, plumage with age and sex.

This study focused on social dominance in the white-throated sparrow, *Zonotrichia albicollis*, an emberizine that congregates in flocks in winter and readily accepts seed at feeding stations (Harrington 1973). This migratory species is abundant in winter in the southeastern U.S. Two morphs occur that differ in colour (Lowther 1961; Thorneycroft 1966, 1975), size (Rising & Shields 1980) and behaviour (Lowther & Falls 1968; Knapton & Falls 1982, 1983). White morphs are reportedly more aggressive than tan morphs in spring (Ficken et al. 1978) and residents tend to be more dominant than migrants (Harrington 1973; Hailman 1975). Watt et al. (1984) reported that sex and morph best predict dominance in captive flocks of this species in winter.

This study had three goals: to identify factors that affected dominance in free-living sparrows of known age and sex; to employ multivariate analy-

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ses to separate intercorrelated factors; and to discuss the possible causes of these factors. Because of the paucity of information on the effect of location on dominating ability in passerines, we examined this factor in detail.

METHODS

Basic Procedures

This research took place during four winters at the Mason Farm Biological Reserve in Chapel Hill, North Carolina. The data presented here were gathered during three winters, 1983–1984 through 1985–1986. From October to April of each year, as well as in 1982–1983, we trapped white-throated sparrows and banded them with unique colour combinations. Sparrows were trapped two–three times each week in 17 six-celled treadle traps baited with millet and spaced roughly 25 m apart along a hedgerow beside overgrown and cultivated fields. When first captured, each bird was weighed (nearest 0·1 g), scored for the amount of subcutaneous fat in its furcular and abdominal regions, checked for skull pneumatization, and sexed by laparotomy (see Wingfield & Farner 1976). Wing chord and the brightness of the median, lateral and superciliary stripes in each bird's crown were measured as described below. Birds were released where captured within 2 h of the time of capture. On days with no trapping, dominance interactions among colour-banded birds were recorded at four observation sites along the trapline. During 1983–1984 through 1985–1986, we trapped and banded 1235 white-throated sparrows. Of this total, 466 birds remained in the study area long enough to be included in the analysis of dominance. Minimum estimates for the numbers of captures in each year of the study are: 4600 in 1983–1984; 3400 in 1984–1985; and 3100 in 1985–1986.

Determination of Adjusted Mass

The masses of wintering passerines vary as they gain subcutaneous fat for the winter and migration (Odum 1949). Thus, the mass of an individual at a given time depends on its size, the amount of fat it has stored and the contents of its digestive tract. Although we could not account for gut contents when calculating mass, it was possible to estimate the amount of subcutaneous fat by scoring the amount of fat visible in the furcular and abdominal regions (Helms & Drury 1960) at the time of each bird's first capture. We regressed fat score against mass for the sample of birds in 1984–1985 ($r^2=0{\cdot}40$, $N=351$, $P<0{\cdot}001$) and adjusted the measured mass of each bird by subtracting from it a number equal to its fat score multiplied by the slope from the regression equation. This adjusted mass is an estimate of a bird's lean mass.

Determination of Age

At Mason Farm no first-winter birds had completed skull ossification before 15 December but most did so in January (mean completion date ± SD = 14 January ± 18 days). All birds captured for the first time after 1 January with ossified skulls were considered to be of unknown age and were excluded from the analysis. All birds first captured on or before 31 December with ossified skulls were considered to be after-first-winter birds. We considered all after-first-winter birds of unknown age to be second-winter birds, since 60% of the comparable birds of known age in the population ($N=384$) were in their second winter. Using these criteria, we estimated that three (4%) of the first-winter birds each year were misclassified as after-first-winter birds and 10 (12%) of the after-first-winter birds were misclassified as second-winter birds. The accuracy with which we knew birds' ages was lowest during the first year of the study and improved from year to year as individuals of known age returned.

Determination of Residency

Only birds that were trapped or observed 60 or more days apart in a winter were regarded as residents of the study area during that winter. Each bird was assigned a residency status based upon the number of previous years it had resided at Mason Farm: first-year resident, second-year resident and so forth. As with age, the accuracy with which residency status was known improved during the course of the study.

First-winter birds could only be first-year residents, while most after-first-winter birds were at least second-year residents. However, 24% ($N=384$) of the after-first-winter birds in the population were first-year residents (newcomers). Therefore, age and residency were strongly, but not perfectly, associated.

Determination of Crown Brightness and Morph

Each bird was scored for brightness of its median, lateral and superciliary stripes in basic plumage at the time of its first capture. The technique used to score these crown stripes is described elsewhere (Piper & Wiley, in press). Briefly, the median, lateral and superciliary stripes on each sparrow were given numbers to indicate where their colour changed from white to tan or grey, from solid black to black with brown flecks, and from white to tan or grey, respectively. The sum of these three numbers for each individual was its overall crown brightness. Birds with bright, black-and-white crowns received high scores for crown brightness, while those with dull, brown-and-tan crowns received low scores.

We identified white and tan morphs in one of two ways. Of the 466 birds included in the analysis, 182 (39%) remained in the study area after the prealternate moult in March and April and were assigned to a morph by inspection of their alternate plumage. Morphs were easily recognizable at this time. For the 284 remaining birds, morph was determined by means of a simple formula based on a bird's age and sex and the brightness of its median and lateral stripes in basic plumage. This formula correctly identified the morphs in the Mason Farm population with a success rate of 89% (Piper & Wiley, in press). Between inspecting 39% of the birds in alternate plumage and using the above formula to identify morphs among birds not captured in alternate plumage, we identified morphs in this study with an estimated success rate of over 93%.

Determination of Fall Arrival Date

The first record of a bird's presence in the study area after its fall migration usually came from trapping. Since individuals varied greatly in the frequency with which they were trapped, the first trapping date is a biased index of a bird's arrival date. Birds that were trapped often appeared to have arrived earlier than those that were seldom trapped. To correct for this bias, we calculated the mean number of days between captures for each bird during a winter and subtracted one half of this mean trapping interval from the date of the bird's first capture each year to produce an estimate of fall arrival date. The mean ± SD estimated arrival date for the resident white-throated sparrows at Mason Farm in 1984–1985 was 27 November ± 27 days ($N=171$).

Determination of Mean Trapping Point

Most birds were captured at only two or three adjacent locations during a winter. The locations of all captures of an individual were used to compute its mean trapping point. We surveyed the trapline with a compass and measuring tape to determine distances and directions between adjacent traps and distances between traps and observation blinds. We then determined the distance from each trap to an arbitrary reference point (the trap at the end of the trapline) and averaged the distances for all of a bird's captures to calculate its mean trapping point. The mean number of captures for resident white-throated sparrows during the study was $12{\cdot}1 \pm 9{\cdot}4$ SD ($N=611$). Birds with fewer than three captures were excluded from this analysis. Three or more captures produced stable estimates of the locations of birds' ranges.

Determination of Sizes of Individuals' Ranges

A common measure of the extent of an animal's movements is the standard deviation of the locations where it is observed (Jennrich & Turner 1969). Since the hedgerow along the trapline was linear, we calculated standard deviations for each bird's trapping locations along the line and used this as an index of the size of its range.

Because traps might fail to cover a bird's range adequately or birds might show preferences for certain traps, we conducted daily censuses from 13 January through 1 April 1986, a period with no trapping, and recorded the locations of each colour-banded white-throated sparrow. We then computed a standard deviation of the census points for each bird during this period and compared it with the standard deviation of trapping points for the same bird from 10 October through 12 January of 1985–1986. The two indices were significantly correlated ($r^2=0{\cdot}35$, $N=126$, $P<0{\cdot}001$), despite the fact that they were calculated for different time intervals. Therefore, trapping data gave a good estimate of the size of a bird's range.

Measurement of Dominance

We recorded dominance interactions from observation blinds at four feeding stations during the months of December through March in 1983–1984 and 1984–1985, and in December and January of 1985–1986. Observation stations were placed at 75- to 100-m intervals along the trapline. Each consisted of a small plywood blind placed 3–4 m from the edge of a thicket. Millet and sunflower seed were provided for the birds on six cinder blocks (20 × 20 × 40 cm) set on end and placed 0·7 m apart in a 2 × 3 matrix, such that two blocks were at the edge of a thicket, two more were 0·7 m from the thicket, and the last two were 1·4 m from the thicket. The blinds were thus 2–3 m from the outermost blocks.

Interactions were observed from 0800 to 1200 hours on days with no trapping. Time was divided between each of the four blinds so that the total number of interactions recorded at any two of the four sites in a given year never differed by more than 30%. Total numbers of interactions recorded in each year exceeded 11 000 in 1983–1984, 21 000 in 1984–1985 and 8000 in 1985–1986.

Dominance interactions resembled those described in related species (Sabine 1949; Balph 1977) and took place on the feeding blocks, in bushes, or on the ground. Five kinds of interactions were recognized. Supplantations, which were replacements of one bird by another, and attacks, which were similar but more rapid, together constituted over 95% of all interactions. Pursuits (Balph 1977), decisive fights (Sabine 1949), and hold-offs, in which one bird did not move in response to the approach of another, were relatively rare. All five kinds of interactions were considered equally indicative of dominance.

We considered one white-throated sparrow dominant to a second if the first had dominated the second in 75% or more of their interactions. We included all dyads that satisfied this criterion in the analysis, even those with only one interaction, because an analysis of observations made in 1982–1983 showed that in 330 of 355 cases (93%) the first dominance interaction observed between two birds was consistent with the remainder of their interactions. However, if neither bird had dominated the other in 75% or more of their interactions, the dyad was considered undefined and excluded from the analysis. Such undefined dyads constituted 5% of the total number of dyads ($N = 6260$ total dyads) in 1984–1985. Since dominance was determined by a single observation in 39% of all defined dyads in 1983–1984 ($N = 4107$ total dyads), an estimated 98% of these dyads were scored correctly.

One common method used to produce an index of social dominance is to calculate the proportion of a bird's interactions in which it is dominant (Kikkawa 1980; Arcese & Smith 1985). In this case, however, the value of the index for a bird can be strongly influenced by its interactions with a few frequently encountered opponents. A second method of computing dominance scores for animals that form nearly linear hierarchies is to rank them (Schjelderup-Ebbe 1922; Sabine 1949; Watt et al. 1984). This technique is difficult to apply to a large number of individuals, because inevitably many dyads never interact during observations. The index of dominance used in this study, termed dominance proportion, was calculated by dividing the total number of individuals that a bird dominated by the total number of individuals with which it interacted, excluding undefined dyads. This index of dominance is thus the proportion of opponents dominated, rather than the proportion of interactions in which a bird was dominant. An analysis of a group of sparrows at a single site in 1983–1984 showed that dominance proportion was closely correlated with rank in a nearly linear hierarchy ($r^2 = 0{\cdot}84$, $N = 38$, $P < 0{\cdot}001$).

In using the proportion of birds dominated as an index of a bird's dominance, we assumed that each sparrow interacted with a random set of opponents. An analysis of dyads at one site in 1983–1984 revealed that the mean dominance proportions of the opponents of individual sparrows varied from 0·71 to 0·42 (mean ± SD = $0{\cdot}55 \pm 0{\cdot}07$, $N = 53$). Moreover, there was a tendency for birds of high dominance to interact disproportionately with birds of low dominance and vice versa ($r^2 = 0{\cdot}39$, $N = 53$, $P < 0{\cdot}001$). This pattern inflated the dominance proportions of dominant birds and deflated those of subordinate birds. To minimize this problem, we included in the analysis only individuals participating in more than 10 defined dyads. The mean numbers of defined dyads per sparrow were 58 ± 23 SD in 1983–1984 ($N = 115$), 62 ± 26 SD in 1984–1985 ($N = 176$), and 37 ± 18 SD in 1985–1986 ($N = 175$). The distribution of dominance proportion, initially non-normal, was transformed using the logit transformation (Snedecor & Cochran 1967) so that it did not differ significantly from normal ($\chi^2 = 2{\cdot}4$, $N = 121$, $P > 0{\cdot}25$ for 1984–1985).

Distance of Interactions from Mean Trapping Point

Although birds tended to concentrate their interactions at one of the four observation sites, most birds (72% in 1985–1986, $N = 175$) interacted at two or more sites. To account for this tendency of birds to interact at different distances from their mean trapping points, we calculated a weighted mean distance between each bird's mean trapping point and the observation sites where it interacted and called this quantity the distance from mean trapping point. A bird with 20 defined dyads at a distance of 20 m from its mean trapping point and 10 more dyads at a distance of 80 m was assigned a distance from mean trapping point of ((20 dyads) (20 m)+(10 dyads)(80 m))/30 dyads=40 m.

Detailed Analysis of the Effect of Location

A preliminary analysis indicated that the location of a bird's interactions relative to its mean trapping point was related to its dominance. Thus, for the set of birds in 10 or more dyads at each of two or more different sites, we computed an index of each bird's loss of dominance with increasing distance from its mean trapping point. We included in this analysis only the data from the two sites at which a bird interacted in the most dyads.

The index of a bird's loss in dominance with distance was

$$(D_N-D_F)/(Q_F-Q_N)$$

where D_N is the logit transformation of dominance proportion at the observation site nearer the bird's mean trapping point; D_F is the transformed dominance proportion at the site farther from the bird's mean trapping point; Q_F is the distance in metres between the farther observation site and the mean trapping point; and Q_N is the distance between the nearer site and the mean trapping point. A positive value indicated that a bird had lower dominance at the site farther from its mean trapping point.

We excluded 24 birds (12% of the total, $N=208$) because the distances between their mean trapping points and the sites where they interacted differed by less than 10 m. We considered the resolution of our index insufficient to distinguish between distances that differed by so little.

Statistical Analysis

Multivariate analyses were used to find the independent variables most closely correlated with a dependent variable. The variables tested were both categorical (age, sex, morph) and continuous (crown brightness, wing chord length, size of range), and therefore we employed analyses of covariance (Hays 1981). Once it became apparent that analyses of covariance and multiple regressions gave similar results, we used multiple regressions for all analyses because of their simplicity. In each analysis, we first used stepwise regression to select the independent variables most strongly correlated with a dependent variable. The programs employed (Systat, Inc., Evanston, Illinois) eliminated variables with significance levels greater than 0·15. Next, we tested all interaction terms among the selected variables for significance and dropped non-significant interaction terms one by one from highest- to lowest-order. We removed from the models any variable not reaching statistical significance and thus arrived at the final models. To ensure that multiple regression and analysis of covariance produced the same results, each final model was reanalysed using analysis of covariance, and the results were compared with those from the regression.

Because the large number of variables in the multivariate analyses made it likely that some might be statistically significant by chance alone, we reduced the significance level to account for this problem by dividing the usual α value by the number of variables in the analysis (the Bonferroni technique; Keppel 1982). We thus used 0·005 (0·05/10) for the significance level for all multivariate analyses except the main analysis for 1984–1985, for which we used an α level of 0·0025 (0·05/20).

Analyses of the Correlates of Dominance

The main analyses performed were stepwise regressions used to find variables correlated with dominance. Transformed dominance proportion was the dependent variable. Independent variables were mass, wing chord, age, sex, crown brightness, morph, fall arrival date, number of years resident, size of range, and distance between a bird's mean trapping point and the site where it interacted. For 1984–1985, 10 additional variables were included for the colours of leg bands (see Burley 1981).

Additional Analyses

To determine if factors correlated with dominance similarly at different observation sites, we analysed each of the four sites separately for the winter of 1984–1985, using the same variables as for the main analyses.

We examined constancy in dominance from year to year by analysing the relationship between a bird's dominance in its first winter (termed first-winter dominance) and in a later winter at the same site. This analysis used dominance of after-first-winter birds as the dependent variable and included as independent variables first-winter dominance and all other variables from the main analyses. Since this sample was small, we pooled data from all 3 years.

A final analysis examined the factors affecting the loss of dominance with distance and used dominance proportion and all of the variables from the main analyses as independent variables.

RESULTS

General

In all 3 years, stepwise multiple regression selected age and distance from mean trapping point as predictors of dominance, and both variables remained in the final models in all 3 years (Table I). In addition, the stepwise procedure selected length of wing chord in 1983–1984 and 1985–1986, and its correlate, sex, in 1984–1985, as correlates of dominance. These two variables also remained in the final models in their respective years (Table I). Finally, the number of years of residence at Mason Farm and fall arrival date were selected in 1983–1984 and 1985–1986, respectively, though neither remained in the final models. Five independent variables (mass, crown brightness, morph, size of range, and, in 1984–1985, colours of leg bands) were excluded from the models in all 3 years. More than half of the variability in dominance was unexplained: r^2 was 0·457 in (1983–1984, 0·504 in 1984–1985, and 0·449 in 1985–1986. No interaction terms were significant in any of the 3 years. In all cases, multiple regressions and analyses of covariance produced the same levels of significance and coefficients with no greater than 10% differences.

Table I. Correlates of dominance in white-throated sparrows in three winters: partial correlation coefficients from multiple regression analyses

		Variable		
Year	*N*	Age	Sex	Distance from mean trapping point
1983–1984	115	0·32*	0·22*	−0·39**
1984–1985	176	0·42**	0·27**	−0·37**
1985–1986	175	0·37**	0·26**	−0·38**

* $P < 0{\cdot}005$; ** $P < 0{\cdot}0005$.

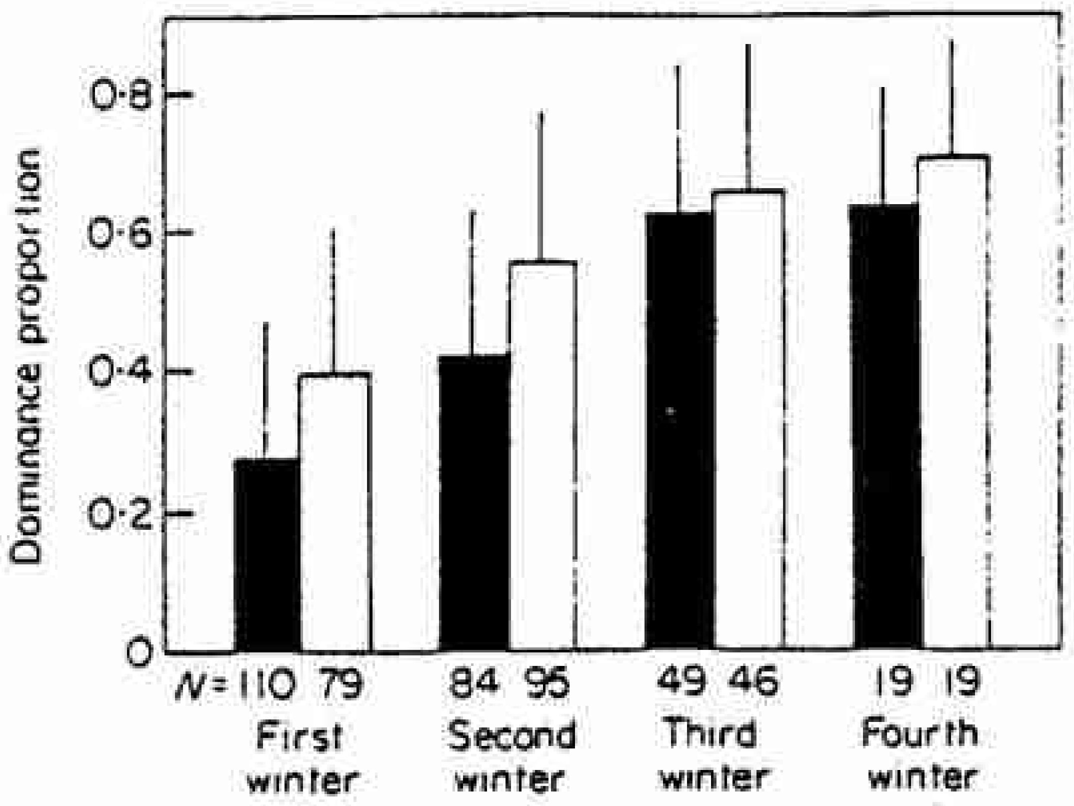

Figure 1. Means and standard deviations of dominance proportion for males and females in four age-classes (all other variables ignored). ■: values for females: □: values for males. See text for results within age- and sex-classes.

Age

Old birds achieved higher dominance status than young birds (Fig. 1). Overall, birds increased markedly in dominance proportion from their first to their second winters (mean increase of 0·19, $t=4{\cdot}71$, $N=174$, $P<0{\cdot}001$ for males; mean increase of 0·21, $t=6{\cdot}76$, $N=194$, $P<0{\cdot}001$ for females), increased somewhat less from their second to their third winters (mean increase of 0·13, $t=2{\cdot}99$, $N=141$, $P<0{\cdot}01$ for males; mean increase of 0·15, $t=3{\cdot}58$, $N=133$, $P<0{\cdot}002$ for females), and did not increase significantly in dominance between their third and fourth winters (mean increase of 0·06, $t=0{\cdot}47$, $N=63$, P ~~<0·05~~ for males; mean increase of 0, $t=0{\cdot}03$, $N=66$, P ~~<0·05~~, for females; see Fig. 1). Although sparrows tended to increase in dominance from year to year, some sparrows lost rank as they became older.

·0·5
·0·5

Number of years of residency in the study area, a variable correlated with age, did not remain in a final model in any year. Thus, it appeared that age itself, rather than association with an area in previous years, was the best predictor of a bird's dominance status.

Sex and Wing Chord

Sex and wing chord were strongly correlated in white-throated sparrows and emerged as almost equally significant but mutually incompatible variables in all 3 years. Moreover, in both sexes after-first-winter birds tended to have longer wings (mean ± SD = 68·4 ± 1·48, $N = 199$ for females; 72·8 ± 1·41, $N = 180$ for males) than did first-winter birds (67·8 ± 1·42, $N = 139$ for females; 71·8 ± 1·38, $N = 116$ for males). To determine if sex or wing chord was the more important correlate of dominance while controlling for the effect of age, we looked at the correlation between wing chord and dominance in six age–sex classes: first-winter females and males, second-winter females and males, and third-winter-and-older females and males. The level for the six tests, determined by the Bonferroni process, was 0·05/6 = 0·008. There was no significant correlation between wing chord and dominance in first-winter ($r^2 = 0·03$, $N = 120$, >0.05 P ~~<0·05~~), second-winter ($r^2 = 0·02$, $N = 84$, >0.2 P ~~<0·02~~), or third-winter-and-older females >0.02 ($r^2 = 0·07$, $N = 68$, P ~~<0·002~~), nor was the correlation significant in first-winter ($r^2 = 0·00$, $N = 90$, >0.2 P ~~<0·02~~), second-winter ($r^2 = 0·07$, $N = 95$, >0.008 P ~~<0·008~~), or third-winter-and-older males >0.05 ($r^2 = 0·06$, $N = 64$, P ~~<0·005~~). Based upon the lack of a correlation between wing chord and dominance within age–sex classes, it appears that sex itself, and not wing chord, best predicted dominance status.

The effect of sex decreased with age (Fig. 1). Among first-winter birds, males had a mean dominance proportion 0·12 higher than females ($t = 3·94$, $N = 189$, $P < 0·001$), while this difference decreased to 0·08 in second-winter birds ($t = 2·18$, <0.05 $N = 179$, P ~~<0·005~~) and to 0·07 for third-winter >0.05 birds and older ($t = 1·78$, $N = 133$, P ~~<0·005~~).

Location

The correlation between distance from mean trapping point and dominance proportion appears to indicate that sparrows dominated opponents more successfully at observation sites near their mean trapping points. It is possible, however, that dominant birds merely settled nearer observation sites than did subordinate birds. If birds dominated opponents more successfully near the centres of their ranges, then those interacting at two or more sites should have had higher dominance proportions at the sites closer to their mean trapping points. Of the 184 sparrows that had 10 or more defined dyads at two sites, 143 (78%) had higher dominance proportions at the site nearer their mean trapping point ($P < 0·001$, sign test). This demonstrates that the dominance of a white-throated sparrow decreased as it interacted farther from the centre of its range (see Fig. 2).

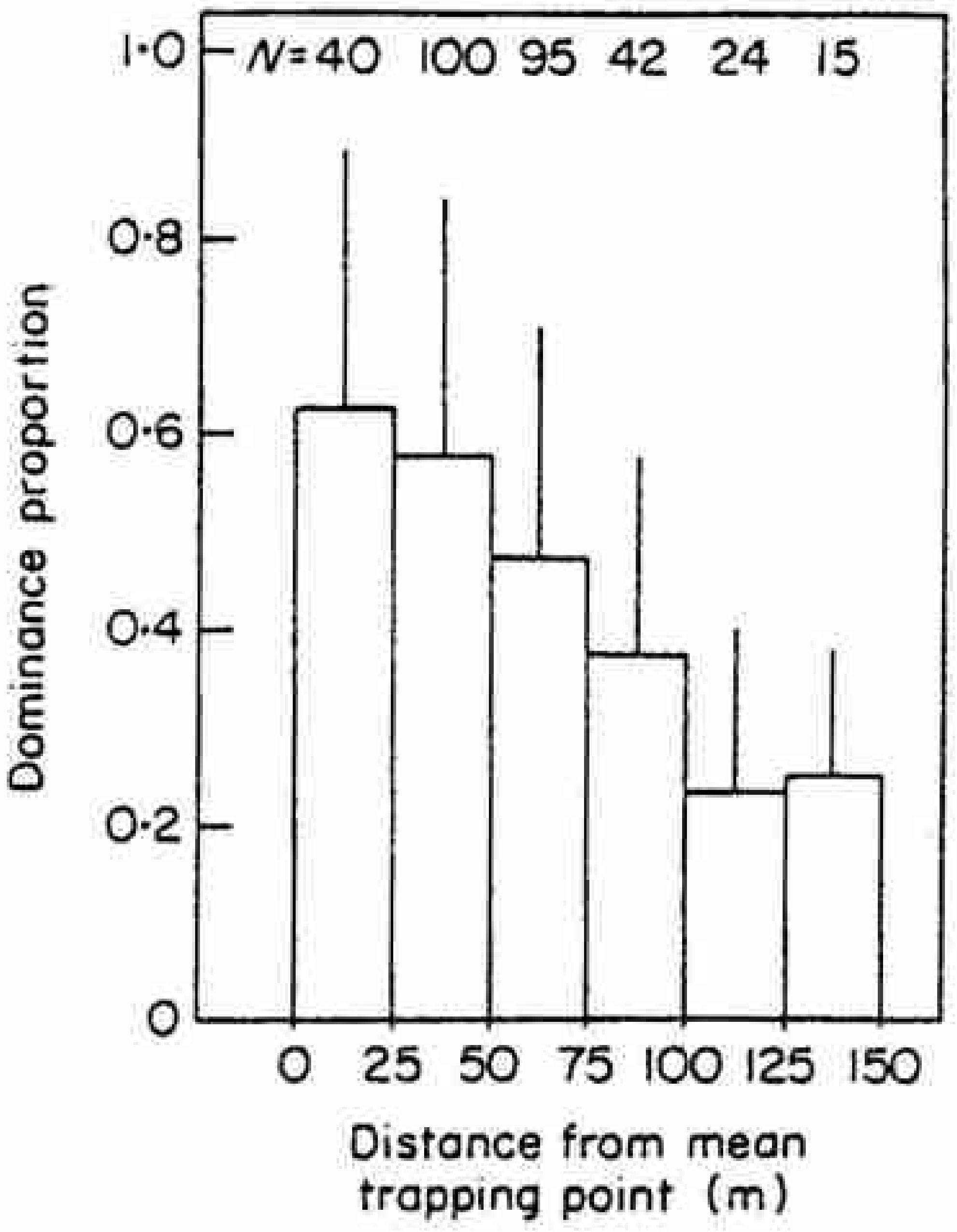

Figure 2. Means and standard deviations of dominance proportion for birds at different distances from their mean trapping points (all other variables ignored).

Site-by-site Analysis

The correlates of dominance did not vary between observation sites in 1984–1985, although correlation coefficients and r^2 values varied somewhat from site to site (Table II).

Constancy in Dominance between Years

The analysis of factors affecting dominance in

Table II. Correlates of dominance in white-throated sparrows at four observation sites in 1984–1985: partial correlation coefficients of age, sex, and distance from mean trapping point

		Variable			
Site	N	Age	Sex	Distance from mean trapping point	r^2 value
1	99	0·43*	0·30*	−0·24*	0·33
2	75	0·53*	0·17	−0·22	0·42
3	69	0·58*	0·18	−0·28	0·41
4	63	0·51*	0·27	−0·34*	0·53

* $P < 0·005$.

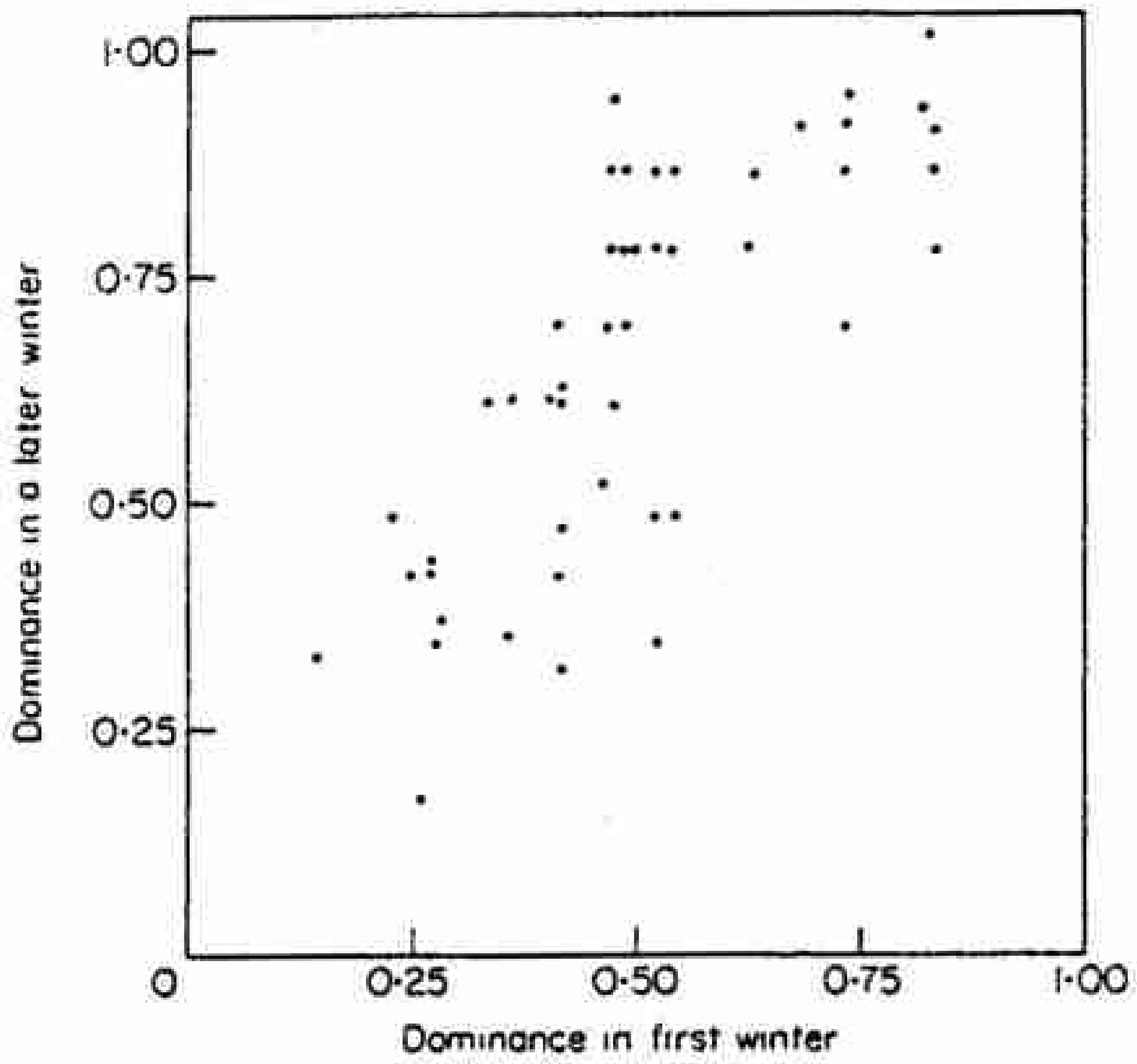

Figure 3. The relation between dominance proportion in a bird's first winter and in a later winter (all other variables ignored).

after-first-winter birds, which included dominance in the first year of life as an independent variable, showed that birds with high dominance status in their first winters tended to retain it in subsequent winters ($r=0{\cdot}36$, $t=3{\cdot}34$, $N=52$, $P<0{\cdot}005$; Fig. 3), and that birds that interacted close to their mean trapping points tended to have high dominance status ($r=0{\cdot}51$, $t=4{\cdot}75$, $N=52$, $P<0{\cdot}005$). No other factor was significant.

Decline in Dominance with Distance

Although only a small amount of the variance was accounted for by the model ($r^2=0{\cdot}17$), birds with high dominance status lost status more rapidly as the distance from the centre of their range increased than did birds with low status ($r=0{\cdot}18$, $t=5{\cdot}76$, $N=184$, $P<0{\cdot}001$). Also birds with short wings lost status more rapidly as the distance from the centre of the range increased than did birds with long wings ($r=0{\cdot}08$, $t=3{\cdot}91$, $N=184$, $P<0{\cdot}001$). Again, it was necessary to consider each sex-class separately to ascertain whether the apparent effect of wing chord was a result of wing chord itself or of sex. The correlation between wing chord and loss in dominance was close to significance in both sexes ($r=0{\cdot}20$, $t=2{\cdot}02$, $N=90$, $P<0{\cdot}05$ for females and $r=0{\cdot}18$, $t=1{\cdot}75$, $N=93$, $P<0{\cdot}10$ for males). Moreover, the r^2 values with sex and wing chord in the model were 0·13 and 0·17, respectively. Hence, it appears that wing chord was the stronger correlate of loss of dominance with distance.

DISCUSSION

A white-throated sparrow's ability to dominate conspecifics was correlated with three main factors: its age, sex and location. Mass, wing chord, crown brightness, morph, fall arrival date, number of years resident in the study area, size of range and colour of leg bands were not correlated with status. The correlates of dominance did not vary between years or from one observation site to another. A sparrow's dominance at a given site in its first winter was a good predictor of its status at the same site in later winters. Finally, birds with short wings and those with high dominance status lost dominance more rapidly at increasing distance from the centres of their ranges than did birds with long wings and birds with low status. The probable causes of these findings are discussed below.

Age

Age was strongly correlated with dominance. In this case, the direction of causation seems clear: age, or some attribute closely related to age, must have affected dominance. Moreover, the age effect apparently did not result indirectly from a bird's prior residency in the area. No previous study has succeeded in separating these two effects, although some studies that have ignored prior residency have reported a correlation between age and dominance (Parsons & Baptista 1980; Fugle et al. 1984).

The proximate cause for the relationship between age and dominance is not clear, and at least two possibilities merit consideration. First, individuals might learn how to dominate opponents as they mature (see Arcese & Smith 1985). Second, dominance might undergo an intrinsic maturation with age independently of a bird's experience. If high dominance status gives a wintering finch an advantage in feeding efficiently (Caraco 1979a, b), storing fat (Fretwell 1969), and remaining safe from predators (Caraco 1979a, b; Schneider 1984), some essential aspect of behavioural ontogeny apparently precludes the attainment of high status in young birds.

Sex

Sex was strongly correlated with dominance proportion in all years and at all sites. This correlation was not an indirect effect of size. Most previous reports of correlates of dominance have not separated these two effects (Balph 1977; Baker & Fox 1978; Watt et al. 1984). Arcese & Smith (1985), however, found no effect of size on dominance within sex-classes in song sparrows, *Melospiza melodia*, and Ketterson (1979a) reported that size and not sex was correlated with dominance in dark-eyed juncos, *Junco hyemalis*.

While sex apparently has a direct effect on dominance in this species, the proximate mechanism is not clear. One possible cause for the greater dominance of males is their higher testosterone levels. Even though circulating titres of testosterone are very low during winter, males of several species, including white-throated sparrows (Archawaranon 1987) have been found to have higher levels of testosterone in the blood than females even during winter (e.g. Schwabl et al. 1984).

Morph

Watt et al. (1984) found a complex relationship between morph and dominance, based upon their study of small groups of white-throated sparrows in aviaries. Their findings suggested that tan morphs attained higher dominance status than white morphs among first-winter birds of both sexes and among after-first-winter females, while white morphs attained higher status among after-first-winter males. We found no evidence of a relationship between morph or winter crown brightness and dominance (Fig. 4).

Watt et al. (1984) found different relationships between morph and dominance in different aviaries. They suggested that a bird resembling the dominant birds in a particular area might dominate other birds more successfully in that area because of this chance similarity in appearance. This argument makes several assumptions about the behaviour of white-throated sparrows, but one of its predictions is that morph should affect dominance differently from one site to another. The site-by-site analysis of dominance in 1984–1985 revealed no correlation between morph and dominance at any of the four sites. Thus, we found no evidence for a site-specific effect of morph on dominance.

Location

Site-dependent dominance

Dominance proportion was strongly correlated with distance from mean trapping point in all years and at all sites. This finding seems particularly significant as the white-throated sparrow is a migratory, flocking bird. Previous reports of site-dependent dominance have all pertained to permanently resident species. Site-dependent dominance among Steller's jays, *Cyanositta stelleri*, for instance, was closely related to the locations of nest sites (Brown 1963), while dominance in magpies, *Pica pica*, is affected by their proximity to natal territories (Eden 1987). Site-dependent dominance in wintering tits (Paridae) takes the form of group-defended territories in areas used for breeding by flock members (Hartzler 1970; Ekman 1979). In contrast, site-dependent dominance in white-throated sparrows cannot result from any continuity in birds' associations with breeding or natal territories or nesting sites.

At least for white-throated sparrows, dominance in winter is not solely an intrinsic ability to dominate conspecifics regardless of location. Many

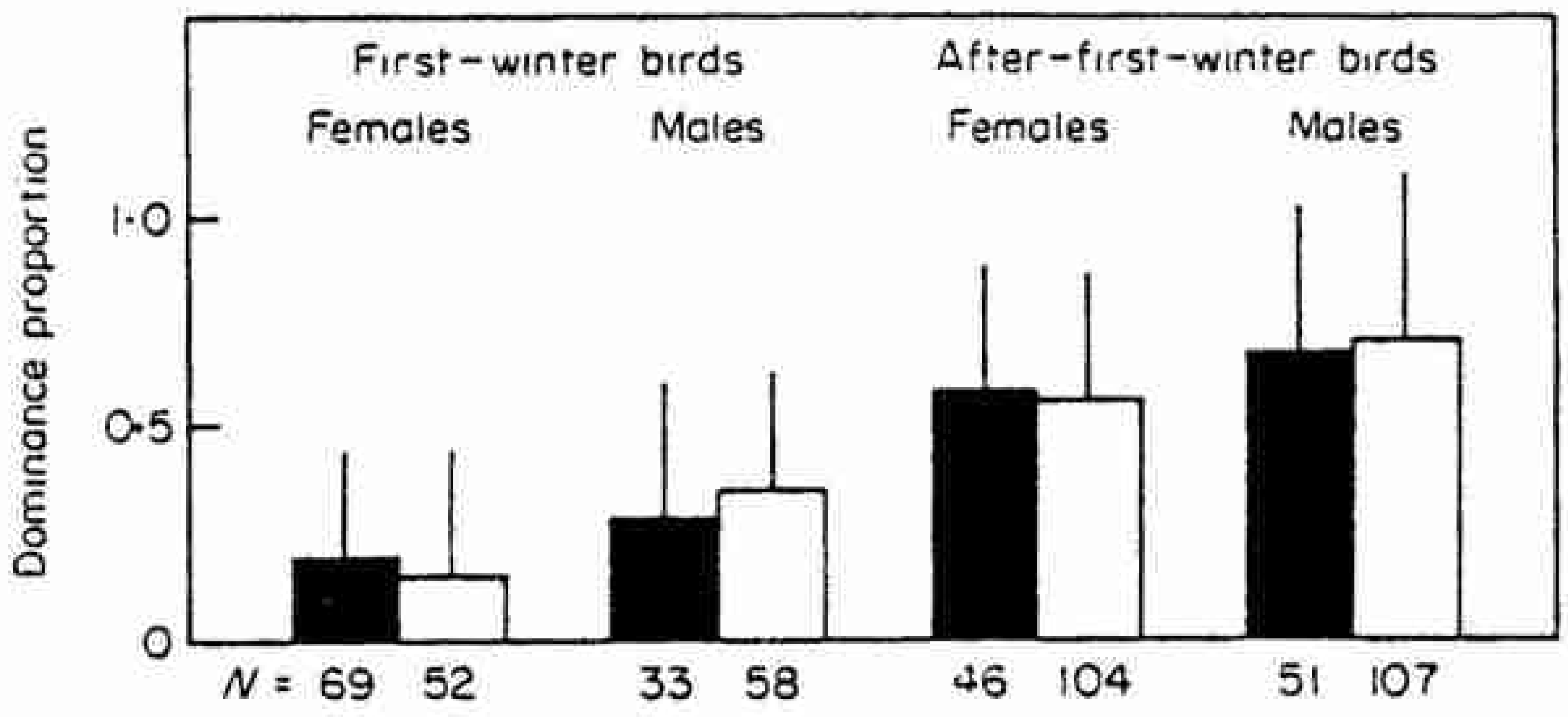

Figure 4. Means and standard deviations of dominance proportion for tan and white morphs within age–sex classes (all other variables ignored). ■: values for tan morphs; □: values for white morphs.

previous studies of avian dominance have implicitly taken this viewpoint (Fretwell 1969; Balph et al. 1979; Ketterson 1979b; Barnard & Sibly 1981; Rohwer & Ewald 1981; Czikeli 1983; Fugle et al. 1984; Schneider 1984; but see also Balph 1979). This study, in contrast, has found that dominance has both intrinsic (age, sex) and situational (site-dependent) components. There have been no previous attempts to detect site-dependent dominance in migratory, flocking emberizines. The importance of this phenomenon in wintering white-throated sparrows suggests that it might also occur in other migratory species.

Evolution of site-dependent dominance

The effect of location appears to be the natural analogue of the cage familiarity effect, or home court advantage, reported in aviary studies (Balph 1979; Yasukawa & Bick 1983). In both the laboratory and the field, birds often enjoy high status in familiar areas. The exact mechanism by which this familiarity is acquired is unknown, although it occurs quite rapidly in some animals (Zayan 1975, 1976).

Yasukawa & Bick (1983), in accordance with predictions from game theory (Maynard Smith & Parker 1976), suggest that the home court advantage evolved as an arbitrary, conventional means of settling dominance disputes and that familiarity with an area in itself confers no advantage to an animal. However, there is evidence indicating that prior knowledge of an area does indeed have advantages for individuals. Ovenbirds, *Seiurus aurocapillus*, for instance, can remember areas where they have foraged successfully in the past (Zach & Falls 1976). Moreover, white-throated sparrows that arrive at Mason Farm early in winter store more fat than those arriving later (Piper 1987). Hence, familiarity with an area seems to allow birds to feed efficiently.

It seems reasonable that familiar areas coincide with areas of high dominance status (those near the centre of a bird's range). A dominant sparrow in a familiar area is presumably able to exploit its knowledge of the food sources of the area efficiently, while a subordinate sparrow in a familiar area would merely serve as a food finder for dominant individuals (Czikeli 1983). Thus, sparrows have probably evolved mechanisms for attaining high status in familiar areas in order to make the best possible use of them.

Territory versus dominance hierarchy

Several workers have suggested that the classical dichotomy between the concepts of territory and dominance hierarchy is an oversimplification (Davis 1958; Sabine 1959; Brown 1963; Waser & Wiley 1980). The strong effect of location reported here, which occurs in a context that is far removed from breeding areas in both space and time, supports the view that site-dependence is a fundamental aspect of aggressive behaviour in species that establish localized ranges.

Waser & Wiley (1980) introduced the term aggression field to define regions in which animals' aggressive tendencies varied from one location to another. Since we measured dominance rather than the tendency to attack or supplant other birds, dominance field is a better term to describe the site-dependent behavioural changes observed in this study. Once one recognizes the site-dependent dominance in white-throated sparrows, it becomes clear that the dominance hierarchies among white-throated sparrows at any one place result from the overlapping of the dominance fields of many individuals. Previous studies that have focused on dominance hierarchies at single locations have failed to consider this possibility. At least in white-throated sparrows, low dominance status at one location does not necessarily indicate low status overall.

Site-dependent dominance and badge-signalling

Rohwer (1977, 1985) suggested that, among Harris sparrows, *Z. querula*, individuals with high dominance status might signal this status with their plumage colour to reduce the need for costly fighting. Ketterson (1979b), Fugle et al. (1984) and Watt (1986) have reported evidence for this phenomenon in other emberizines. Such plumage badges are capable of signalling only the intrinsic (age- and sex-dependent) component of dominance and not the situational (site-dependent) component. Until it is known to what extent situational factors affect dominance in species thought to show badge-signalling, it will be impossible to evaluate the badge-signalling hypothesis completely.

Decline in dominance with distance

The fact that large birds maintain their dominance more successfully than do small birds at increasing distances from their mean trapping points suggests that unfamiliar opponents might use size as an index of dominance. Unlike the plumage badges thought to signal status in other passerines (Rohwer 1977; Balph et al. 1979; Ketterson 1979b; Parsons & Baptista 1980; Fugle et al. 1984; Jarvi & Bakken 1984; Rohwer 1985; Watt 1986), size is not easily bluffed. Maynard Smith & Parker (1976) have shown that if contestants for a resource can estimate their own sizes relative to their opponents', then size can become a conventional signal of dominance among unfamiliar individuals, even if size itself is a poor predictor of dominance.

At first it appears contradictory that size affects loss in dominance with distance, while sex, rather than size, affects dominance in general. This apparent contradiction can be resolved by considering the context in which the two correlations occur. Near a bird's mean trapping point, it is likely to encounter the same individuals repeatedly. Hence the dominance relationships near a bird's mean trapping point should result from many encounters between two individuals, during which each bird has ample opportunity to assess the dominance of the other. On the other hand, at sites far from a bird's mean trapping point, where an individual is not well known, its opponents are likely to assess its dominance by a quick inspection of the bird's appearance. In the absence of any clear sexual dimorphism, size is the only possible morphological aspect that can serve as such an index. Such encounters, when a regular feature of a species' behaviour, might foster status-signalling (Rohwer 1977).

Based upon the pattern of dominance loss with distance, one can make two predictions regarding the local movements of white-throated sparrows. First, small birds should move infrequently, because they lose dominance as they move away from their mean trapping points. Second, birds with high status, which can feed efficiently near their mean trapping points, should tend to remain there, while subordinate sparrows should move more readily.

First-winter Dominance

This analysis showed that a large component of a white-throated sparrow's dominance is determined early in its life. Clearly this component must account for some of the 50% of the sample variance not explained by the three main analyses, none of which included first-winter dominance as a variable. There are two possibilities for explanations of this early influence on dominance. First, individual white-throated sparrows might differ genetically in dominance, as in several species of Galliformes (Craig et al. 1965; Moss & Watson 1980; Boag 1982). Second, birds that hatch and mature early in a breeding season might dominate those that hatch and mature later (Rushen 1982; Arcese & Smith 1985; Kikkawa et al. 1986). The tendency for an individual to maintain a similar dominance status between winters means that each bird tends to face a constant social situation throughout its life.

In summary, this analysis of factors related to dominance in wintering white-throated sparrows has identified an effect of location on dominance, has pinpointed age and sex as intrinsic factors affecting dominance, and has shown that factors early in a sparrow's life influence the dominance it achieves later.

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Errata

Piper, W. H. & Wiley, R. H. Correlates of dominance in wintering white-throated sparrows: age, sex and location. *Anim. Behav.*, 1989, **37**, 298–310.

It is regretted that errors were introduced during the final stages of production on pages 303 and 304 of the Results section. The paragraphs are reprinted below with the corrected results highlighted in bold print.

Age

Old birds achieved higher dominance status than young birds (Fig. 1). Overall, birds increased markedly in dominance proportion from their first to their second winters (mean increase of 0·19, $t=4·71$, $N=174$, $P<0·001$ for males; mean increase of 0·21, $t=6·76$, $N=194$, $P<0·001$ for females), increased somewhat less from their second to their third winters (mean increase of 0·13, $t=2·99$, $N=141$, $P<0·01$ for males; mean increase of 0·15, $t=3·58$, $N=133$, $P<0·002$ for females), and did not increase significantly in dominance between their third and fourth winters (mean increase of 0·06, $t=0·47$, $N=63$, $\mathbf{P>0·5}$ for males; mean increase of 0, $t=0·03$, $N=66$, $\mathbf{P>0·5}$ for females; see Fig. 1). Although sparrows tended to increase in dominance from year to year, some sparrows lost rank as they became older.

Number of years of residency in the study area, a variable correlated with age, did not remain in a final model in any year. Thus, it appeared that age itself, rather than association with an area in previous years, was the best predictor of a bird's dominance status.

Sex and Wing Chord

Sex and wing chord were strongly correlated in white-throated sparrows and emerged as almost equally significant but mutually incompatible variables in all 3 years. Moreover, in both sexes after-first-winter birds tended to have longer wings (mean ± SD $=68·4\pm1·48$, $N=199$ for females; $72·8\pm1·41$, $N=180$ for males) than did first-winter birds ($67·8\pm1·42$, $N=139$ for females; $71·8\pm1·38$, $N=116$ for males). To determine if sex or wing chord was the more important correlate of dominance while controlling for the effect of age, we looked at the correlation between wing chord and dominance in six age–sex classes: first-winter females and males, second-winter females and males, and third-winter-and-older females and males. The level for the six tests, determined by the Bonferroni process, was $0·05/6=0·008$. There was no significant correlation between wing chord and dominance in first-winter ($r^2=0·03$, $N=120$, $\mathbf{P>0·05}$), second-winter ($r^2=0·02$, $N=84$, $\mathbf{P>0·2}$), or third-winter-and-older females ($r^2=0·07$, $N=68$, $\mathbf{P>0·02}$), nor was the correlation significant in first-winter ($r^2=0·00$, $N=90$, $\mathbf{P>0·2}$), second-winter ($r^2=0·07$, $N=95$, $\mathbf{P>0·008}$), or third-winter-and-older males ($r^2=0·06$, $N=64$, $\mathbf{P>0·05}$). Based upon the lack of a correlation between wing chord and dominance within age–sex classes, it appears that sex itself, and not wing chord, best predicted dominance status.

The effect of sex decreased with age (Fig. 1). Among first-winter birds, males had a mean dominance proportion 0·12 higher than females ($t=3·94$, $N=189$, $P<0·001$), while this difference decreased to 0·08 in second-winter birds ($t=2·18$, $N=179$, $\mathbf{P<0·05}$) and to 0·07 for third-winter birds and older ($t=1·78$, $N=133$, $P>0·05$).