

The relationship between social dominance, subcutaneous fat, and annual survival in wintering white-throated sparrows (*Zonotrichia albicollis*)

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Summary. We used multivariate analysis to identify factors correlated with level of subcutaneous fat (a form of stored energy) in a migratory, wintering population of white-throated sparrows. Dominant birds, residents from previous years, and birds residing in certain regions of the study area tended to have high mean fat levels during January and February. On the basis of differences in levels of fat, dominant prior residents could probably survive 50% longer without food than subordinate newcomers. An additional analysis revealed that dominant sparrows returned more frequently to the study area than subordinates, a result that might indicate higher survival.

Introduction

In studying the ecological consequences of social dominance in wintering birds, it is important to determine how dominance affects survival. However, it is difficult to study patterns of survival directly because mortality usually cannot be distinguished from emigration. The tendency of many wintering birds to store fat during winter (Baldwin and Kendeigh 1938; Odum 1949; Helms and Drury 1960; Dawson and Marsh 1986) provides a potential solution to this problem. Level of subcutaneous fat might serve as an indirect index of survival because it reflects a bird's ability to avoid starvation (King 1972; Blem 1976; Ketterson and King 1977; Nolan and Ketterson 1983).

Ground-feeding birds in temperate regions often rely upon fat storage for survival in winter, when snow can prevent feeding for prolonged periods (Rogers 1987). Studies of two ground-feeding

emberizines, white-crowned sparrows (*Zonotrichia leucophrys*) and dark-eyed juncos (*Junco hyemalis*), have revealed that heavy individuals can survive periods of fasting longer than light birds (Ketterson and King 1977; Steube and Ketterson 1982), an indication that fat reserves, which constitute up to 25% of the body mass of such birds in winter (Odum 1949), can affect survival.

We present here the results of a multivariate analysis of the relationships between fat levels and various behavioral and morphological attributes, including social dominance, in a population of white-throated sparrows (*Zonotrichia albicollis*). In addition, we analyze attributes related to the tendencies of individuals to return to our study area from year to year.

Methods

Trapping regimen and basic measurements

White-throated sparrows were captured two or three times weekly from November through April of 1982 to 1988 at Mason Farm Biological Reserve in Chapel Hill, North Carolina; however, the analysis of fat levels is based solely on data from 1984 to 1985, the year for which data are most complete. We trapped birds in six-celled treadle traps at 17 stations approximately 25 m apart along a nearly straight hedgerow (Piper and Wiley 1989a). Traps were baited with about 15 ml of millet on the day prior to trapping. At about 0800 h on each trapping day, we again baited each cell with roughly 15 ml of millet and set the traps. Approximately 1 h later, we recorded identities and fat scores (see below) of all white-throated sparrows found in the traps and the time of day, placed unbanded birds in bags so that they could be weighed and measured later, and reset the traps for the next trapping run. We made either two or three such runs during the morning on each trapping day.

The following measurements were taken on each white-throated sparrow when first captured: length of unflattened wing chord (to nearest 0.5 mm), extent of skull pneumatization, mass (to nearest 0.5 g), and brightness of median, lateral, and superciliary stripes in the crown (extent of pure white or black as opposed to tan or brown, see Piper and Wiley 1989b). In

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addition, the sex of each bird was determined by laparotomy (Wingfield and Farner 1976). Afterwards, each bird was returned to the location of its capture and released.

Morph, age-class, residence-class, fall arrival date, and region of the trapline where a bird's mean trapping point was located were determined using data from measurements or captures (see Piper and Wiley 1989a). We identified white and tan morphs based on the brightness of crown stripes (Piper and Wiley 1989b). Age-class (first-, second-, third-, or fourth-winter) was determined from the extent of a bird's skull pneumatization in the year it was first captured. We assigned birds to winter residence-classes (first-, second-, and third-year) based on the number of winters they were known to have resided in the study area. Birds trapped or observed in the study area for a period of more than 60 days during any winter were considered residents. We estimated each individual's date of arrival in our study area each year by subtracting one-half of its mean interval between captures from the date of its initial capture. Finally, the trapline was arbitrarily divided into four segments of equal length and each sparrow was assigned to the one of these regions in which its mean trapping point was located.

Determination of dominance

Dominance interactions between color-banded sparrows were recorded at four feeding sites along the trapline from 1983 to 1987. One bird was considered dominant to another if it dominated that bird in 75% or more of their interactions. As an index of dominance we used dominance proportion, i.e., the number of sparrows dominated by a bird divided by the total number of birds to which it was dominant or subordinate (Piper and Wiley 1989a). We excluded from the analysis all sparrows seen to interact with fewer than 10 other individuals (mean number of observed opponents = 62 ± 26 SD). The distribution of dominance proportion was normalized with the logit transformation (Snedecor and Cochran 1967).

Scoring of subcutaneous fat

We scored subcutaneous fat in the furcular and abdominal regions on a scale similar to that of Helms and Drury (1960). The scores for fat in the furcular cavity were defined as follows: 0 = no fat visible; 1 = fat visible but not reaching the upper margins; 2 = cavity entirely lined with fat to the upper margins, but still concave; 3 = cavity filled with fat to the level of the pectorialis muscle; 4 = convex mound of fat protruding above the level of the muscle. Fat over the abdominal wall was also scored on a 4-point scale as follows: 0 = no fat visible; 1 = fat covering one-fourth of the surface of the abdomen; 2 = fat covering one-half of the surface; 3 = fat covering three-fourths of the surface; 4 = fat completely covering the wall. We also recognized half scores between the classes described above. A bird's combined fat score, which ranged from 0 to 8, was the sum of its furcular and abdominal scores.

Determination of time of capture and use of artificial food

Levels of subcutaneous fat in wintering passerines increase steadily during the course of a day (Helms et al. 1967; Helms and Smythe 1969; Nolan and Ketterson 1983). Because 88% of all captures in our study occurred between 0800 h and 1200 h, time-related variability was likely to be minimal. However, to control for any remaining variation among individuals in times of capture, we calculated a mean hour of capture in January

and February for each individual and included it as a predictor variable in the analysis of fat scores. To control for a possible effect of the supplemental food on fat levels, we used the number of an individual's captures and the number of its opponents in dominance interactions as indications of their use of food at traps and observation sites, respectively, and included these variables in the analysis of fat levels.

Analysis of fat scores

In selecting indices of fat storage, we assumed that the risk of starvation was greatest in January and February, the two coldest months at our study area. Three indices of fat storage were computed for each individual: the mean and the maximal fat score during January and February and the fat score on 26 January 1985, the date on which we captured the greatest number of individuals.

To examine correlates of the three indices of fat storage, we used each index as a criterion (dependent) variable in a separate analysis. Predictor (independent) variables included: dominance proportion, age, sex, morph, brightness of the crown in basic plumage, length of wing chord, number of years resident at Mason Farm, fall arrival date, mean hour of capture, region in which a bird's mean trapping point was located, number of opponents in dominance interactions, and number of times trapped.

Since the predictor variables were both categorical (e.g., age, sex, morph) and continuous (e.g., crown brightness, wing chord, mean trapping hour), we used an analysis of covariance (Hays 1981). Initially, however, stepwise multiple regressions (with $\alpha = 0.15$ used as the criterion for selection; Systat Inc., Evanston, Ill) with backwards elimination (Draper and Smith 1966) were employed to select the best correlates of fat among the predictor variables and their interactions. The α level was reduced to 0.004 to account for the large number of variables included (the modified Bonferroni method, see Keppel 1982).

Analysis of year-to-year return rates

Within-year survival was difficult to determine in our population because of the uncertainty of trapping individuals from month to month. Instead, we carried out a discriminant analysis on birds in four winters (1983–1987) to determine attributes in a given winter associated with the tendency to return to the study area in the following winter. The criterion variable indicated whether a bird "returned" or was "missing" in the subsequent year. (None of the 788 birds in the analysis was observed to reappear after having been missing during one winter.) A stepwise discriminant analysis was used to choose the best correlates among ten predictor variables: dominance proportion, mean fat score in January and February, age, sex, morph, crown brightness, length of wing chord, number of year's residence, fall arrival date, and region of mean trapping point. The same procedure used in the analysis of fat was followed to select correlated variables (with an α level of 0.005), and the discriminant function was obtained from the values of r^2 and N (see Kleinbaum and Kupper 1978).

Results

Analysis of fat levels

The three indices of fat storage (mean fat, maximum fat, and fat on 26 January) had similar corre-

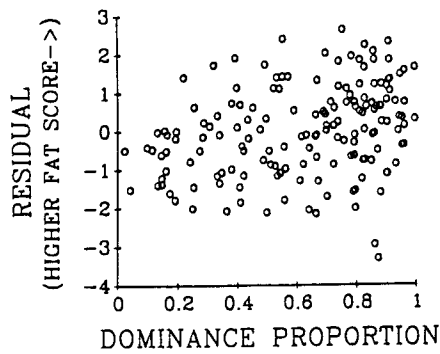


Fig. 1. Relation between dominance proportions and residuals from the linear model of mean fat scores that included only length of residence and region as predictors. With the effects of residence and region controlled, dominant birds had higher fat scores than subordinates

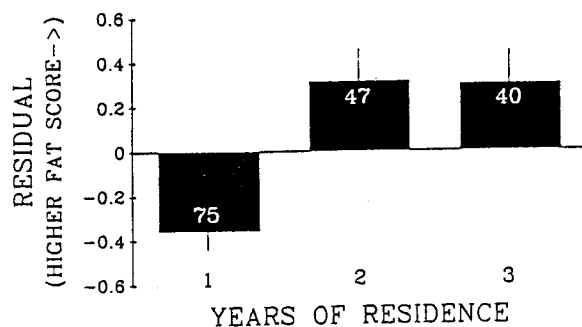


Fig. 2. Means \pm SE of residuals from the linear model of mean fat scores that included only dominance proportion and region as predictors. Residuals are grouped by residence-class. With the effects of dominance and region controlled, second- and third-year residents had higher fat scores than newcomers

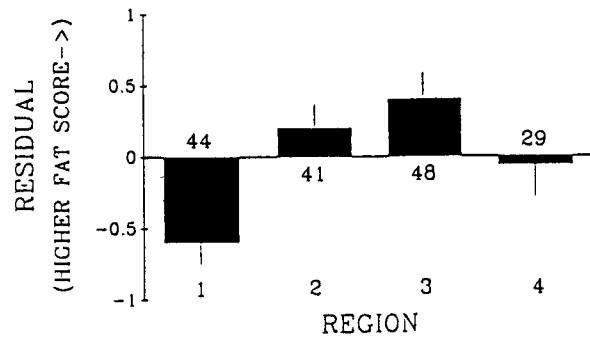


Fig. 3. Mean \pm SE of residuals from the linear model of mean fat scores that included only dominance proportion and residence as predictors. Residuals are grouped by region of the study area. With the effects of dominance and residence controlled, fat scores varied between regions

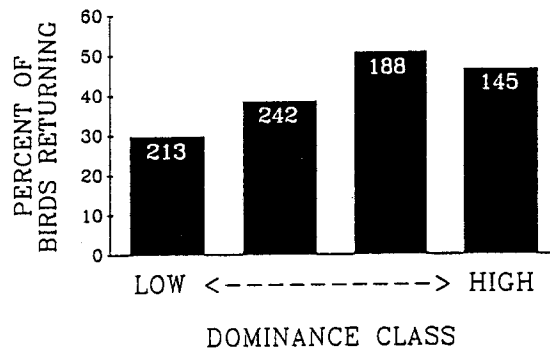


Fig. 4. Percentages of birds in four quartiles of dominance proportions that returned in a subsequent year. The figure indicates that dominant birds returned to the study area more often than did subordinates

lates, and no interaction term was significant in any analysis. Because of the relatively large R^2 value and sample size ($R^2=0.424$ and $n=162$) for the analysis of mean fat (maximum fat, $R^2=0.258$, $n=162$; fat on 26 January, $R^2=0.442$, $n=92$), we will describe here only the results from the analysis of mean fat.

This analysis revealed that individuals with high dominance proportions ($F_{1,156}=24$, $P<0.0005$; Fig. 1) and prior residents ($F_{1,156}=17$, $P<0.0005$; Fig. 2) tended to have high fat levels. Moreover, mean fat level varied significantly among regions ($F_{3,156}=7.7$, $P<0.0005$; Fig. 3). Fall arrival date, morph, number of opponents in dominance interactions and number of captures, though initially selected by the stepwise procedure, all failed to reach significance at the 0.004 level and together accounted for only an additional 5% of the variance.

To ensure that the partial correlation between

prior residence and fat level resulted from residence itself and not age (a close correlate, see Table 1), we examined the relationships between residence and fat within a large age-class and between age and fat within a large residence-class. The effect of residence persisted among second-winter birds ($r=0.29$, $t=2.25$, $P=0.03$, $n=50$), while age had no effect among second-year residents ($r=0.09$, $t=0.84$, $P=0.40$, $n=75$).

Analysis of return rates

Of all the predictor variables examined for correlations with the tendency to return to the study area, only dominance proportion was significant. Dominant birds showed a slight but highly significant tendency to return at a higher rate than subordinates overall ($r=-0.15$, $R^2=0.022$, $P<0.0005$, $n=788$; Fig. 4); this trend was present in every year ($r=-0.16$, -0.12 , -0.16 , -0.16 and $n=$

Table 1. Matrix of correlations between all variables examined in the analysis of fat levels

	Dom.	Age	Sex	Morph	Crown	Wing	Resid.	Arr. date	Hour of capt.	Region	Dyads	No. of capt.
Dominance proportion	1.000	0.561	0.241	-0.135	0.186	0.381	0.496	0.087	-0.052	-0.021	0.156	-0.454
Age	-	1.000	0.018	-0.109	0.239	0.167	0.881	0.122	0.058	0.013	-0.140	-0.660
Sex	-	-	1.000	-0.032	0.382	0.839	0.056	-0.221	-0.072	-0.061	0.044	-0.074
Morph	-	-	-	1.000	-0.650	-0.089	-0.008	-0.169	-0.136	0.292	0.107	0.089
Crown brightness	-	-	-	-	1.000	0.379	0.1188	-0.173	0.166	-0.115	-0.142	-0.111
Length of wing chord	-	-	-	-	-	1.000	0.188	-0.088	-0.003	0.080	0.014	-0.232
Length of residence	-	-	-	-	-	-	1.000	0.062	0.018	0.104	-0.108	-0.635
Fall arrival date	-	-	-	-	-	-	-	1.000	0.049	-0.191	-0.147	-0.193
Mean hour of capture	-	-	-	-	-	-	-	-	1.000	-0.061	-0.144	-0.083
Region	-	-	-	-	-	-	-	-	-	1.000	-0.019	-0.005
Number of dyads	-	-	-	-	-	-	-	-	-	-	1.000	0.252
Number of captures	-	-	-	-	-	-	-	-	-	-	-	1.000

144, 207, 206, 231 in 1983 to 1987, respectively). The discriminant function, $L = 6.67 - (0.203)(D)$, where D is the logit dominance proportion, allows return to be predicted successfully for 60% of the sparrows, as compared to 52% if predictions are made randomly (cutoff value for $L = 6.22$).

In none of the 4 years, nor in the 4 years combined, was mean fat score in January and February a significant predictor of tendency to return in the following years.

Discussion

Effects of fat storage on survival

A critical assumption made during this study was that fat scores reflected overall fat content. The assumption appears justified because the amount of fat stored in the furcular and abdominal regions has been shown to indicate overall fat level in white-throated sparrows (Odum and Perkinson 1951) and, in this species and two other emberizines, furcular and abdominal fat are strongly correlated with mass (Wolfson 1954; Helms and Drury 1960).

We also assumed that the amount of fat stored by a wintering bird was proportional to the length of time it could survive without food. Although fat reserves are clearly an important source of energy during cold periods when food is scarce (King 1972; Blem 1976; Dawson et al. 1983), no study has directly compared fat levels before fasting with survival during fasting. However, studies have shown that survival during fasting is proportional to mass before fasting in three wintering emberizines (Ketterson and King 1977; Steube and Ketterson 1982), which suggests that fatter birds survive longer. Fat is likely to be especially important to white-throated sparrows, which feed almost exclusively on the ground during midwinter and must therefore endure occasional fasting after snowfalls (Rogers 1987).

While fat apparently provides important insurance against starvation, it also increases mass and thus might reduce maneuverability during escapes from predators (King 1972; Nolan and Ketterson 1983; Lima 1986). White-throated sparrows, which normally remain within 1 m of protective cover while feeding and quickly fly to cover when attacked (Schneider 1984), seem likely to suffer less from a slight reduction in maneuverability than other emberizines, like juncos, *Junco* spp. and vesper sparrows *Poocetes gramineus* (Pulliam and Mills 1977), which feed in more open areas where prolonged chases by predators might occur.

The effect of artificial feeding on fat levels

Food provided during winter can increase survival in wintering passerines (Jansson et al. 1981; Millikan et al. 1985; Brittingham and Temple 1988; Desrochers et al. 1988) and might affect fat levels. This did not appear to be the case in our study. Neither the number of opponents in dominance interactions nor the number of times trapped, indications of a bird's use of supplemental food at observation sites and traps, respectively, was significantly correlated with fat levels.

The effect of dominance

The correlation between fat reserves and dominance proportions indicates either that dominance affected fat reserves, that a bird's fat reserves affected its dominance, or that both were influenced by some other factor. It is unlikely that fat influenced dominance because our observations indicated that most dominance relationships formed in November and December, when fat levels were uniformly low. Thus, unless some undetected factors are involved, this result appears to demonstrate that dominance itself influences fat storage in wintering white-throated sparrows.

Though several other studies have reported higher body masses or fat levels among dominants during winter, these reports lacked clear ecological interpretations because they involved captive birds (Baker and Fox 1978; Wiedenmann and Rabenold 1987) or failed to distinguish dominance from confounding factors such as sex and age (Fretwell 1969; Baker and Fox 1978; Lundberg 1985; Millikan et al. 1985; Wiedenmann and Rabenold 1987).

Dominant white-throated sparrows enjoy two advantages that might allow them to store more fat than subordinates. First, dominant birds might simply obtain more or better food by supplanting subordinates (Caraco 1979; Barnard and Sibly 1981; Czikeli 1983) and thus build up larger fat deposits. Second, dominants might store more fat because they waste less energy avoiding conspecifics while feeding and carrying out other daily activities (Caraco 1979; Baker et al. 1981; Millikan et al. 1985; Waite 1987).

Since food shortages resulting from snowfalls must be a severe risk to subordinates, which acquire less of the scarce food available at such times, one might have predicted that subordinates would store more fat than dominants in order to reduce this threat (see Lima 1986). Apparently subordinates are simply unable to acquire enough food

to guard against starvation without exposing themselves to severe predation risk.

The effect of prior residence

Residents from previous winters had higher fat levels than newcomers. Since age was not significantly correlated with fat overall or within an age-class (see "Results"), it seems clear that residence is the stronger correlate.

The relationship between fat levels and residence might have occurred because birds that successfully found food in the study area (i.e., fatter birds) tended to return in subsequent winters. However, our results showed that mean fat level was not related to probability of return, and thus our data do not support this interpretation. The correlation appears to indicate that some individuals can store more fat because of having resided in an area in a previous winter.

The most obvious explanation for this effect of prior residence is that birds with prior experience in the area remembered the locations of food and/or other features of their ranges from one winter to the next, and as a result, were able to store more fat than newcomers to the area. Ovenbirds (*Seiurus aurocapillus*) and Clark's nutcrackers (*Nucifraga columbiana*) can remember locations of food for a day and several months, respectively (Zach and Falls 1976; vander Wall and Balda 1981), but no study to date has explored the possibility that a migratory species can remember details of its winter range from one year to the next.

It is important to note that the fat levels of third-year residents were no higher than those of second-year residents, when the effects of dominance and region were controlled (see Fig. 2). If learning about a winter range does occur, it appears that an individual learns no more useful information about its winter range after one season of residence.

The effect of region

The relationship between mean fat level and region of the study area (Fig. 3) indicates that white-throated sparrows did not find food equally available in these areas and thus did not settle in regions in proportion to food availability. This might have occurred because birds settled in winter ranges without regard to the availability of food (Fretwell 1972). A second possibility is that individuals' ranges were adjusted to the availability of food in the fall, when berries were the major food, and

thus had little relation to availability of food during midwinter, when seeds on the ground constituted most of the diet.

Duration of survival based on fat scores

Differences in fat levels resulting from dominance, prior residence, and regions of the study area imply that birds should differ in their abilities to survive periods of cold and snow. To assess the possible consequences of these differences, we estimated the length of time that individuals were likely to survive periods of fasting based on three assumptions: fat scores were proportional to total fat reserves, length of survival was proportional to total fat reserves, and sparrows with the smallest fat reserves (2.0 units of fat) could survive only overnight and a few hours of the next morning (16 h in all) without food (King 1972, Blem 1976). Thus we assumed that each unit of fat score allowed 8 h of survival without food.

Given these assumptions, individuals varied from 16 h (mean fat score of 2.0) to 61 h (mean score of 7.6) in the length of time they could survive without food in winter conditions. Our estimate of the maximal duration of survival is close to the 3 nights and 2 days found for captive white-crowned sparrows (Ketterson and King 1977) and dark-eyed juncos (Steube and Ketterson 1982). Among white-throated sparrows, a typical dominant prior resident (mean fat score=5.6; see Fig. 5) should be able to survive 45 h of fasting during winter, while a typical subordinate newcomer (Mean score=3.7; Fig. 5) should be able to survive 30 h. Since snow can prevent birds from foraging on the ground for 2 or 3 days during

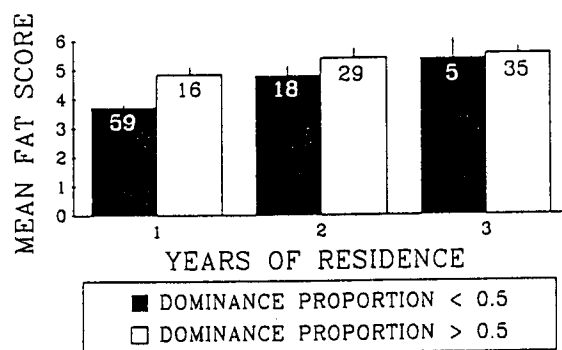


Fig. 5. Means \pm SE of fat scores in January and February by dominance- and residence-class (all other variables ignored). The figure indicates that fat scores increased steadily with increasing dominance and length of residence

January and February in North Carolina, it seems likely that dominance and prior residence can have an important effect on chances of survival in winter.

Annual return rates and survival

The tendency for dominant birds to return more frequently than subordinates might result from lower survival of subordinates, from a trapping bias, or from lower site fidelity among subordinates. The second possibility is not supported by our data. Birds with below-average dominance were trapped more often (mean number of captures = 12.0 ± 9.8 SD, $n=410$) than those with above-average dominance (mean = 9.1 ± 8.4 SD, $n=386$), and the 4.6% of all returns ($n=421$) recorded at observation sites but not captured in traps constituted a group with higher than average dominance ($t=3.35$, $P<0.01$, two-tailed test). The third possibility seems more plausible. Subordinate white-throated sparrows tend to abandon winter ranges when food levels drop (Piper 1987), so subordinates from previous years might have left the study area early in winter and thus avoided detection. However, if such emigration had contributed to the correlation between return rate and dominance, then the correlation should have been strongest near the ends of the trapline, since birds at the ends of the trapline could escape detection by moving short distances. In fact, the correlation is weaker at the ends ($r=-0.12$, $P=0.068$, $n=225$ in region 1 and $r=-0.13$, $P=0.138$, $n=134$ in region 4) than in the interior of the trapline ($r=-0.19$, $P=0.025$, $n=140$ in region 2 and $r=-0.21$, $P=0.004$, $n=184$ in region 3).

The simplest explanation for the relationship between dominance and tendency to return is that dominant birds simply survived better than subordinates. Though dominants have been reported to have higher survivorship than subordinates in wintering passerines (e.g., Baker and Fox 1978; Kikkawa 1980), most of these reports have distinguished neither between mortality and emigration nor between dominance and other, confounding variables (but see Desrochers et al. 1988). Our data indicate that dominance itself results in a high return rate in white-throated sparrows.

It is tempting to conclude that the higher fat levels of dominant birds (see Fig. 1) resulted in higher survivorship between years, but we found no correlation between fat levels and probability of return. The absence of such a correlation might

have resulted in part from the below-normal snowfall (35% below the annual mean) during the 4 years of the study, which probably reduced the benefit of high fat levels. It seems clear, however, that dominance must increase survivorship by some means other than, or in addition to, accumulation of fat in winter. For example, dominant white-throated sparrows might be killed less often by predators because they feed in safer areas during winter (Schneider 1984; Piper 1989), or dominance might improve chances of survival during the breeding season or migration.

In conclusion, our data indicate that for white-throated sparrows, the ability to dominate conspecifics during winter increases the likelihood of survival after snowfalls as a result of greater fat storage and, in addition, leads to higher annual survival.

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References

- Baker MC, Fox SF (1978) Dominance, survival, and enzyme polymorphism in dark-eyed juncos, *Junco hyemalis*. *Evolution* 32:697-711
- Baker MC, Belcher CS, Deutch LC, Sherman GL, Thompson DB (1981) Foraging success in junco flocks and the effects of social hierarchy. *Anim Behav* 29:137-142
- Baldwin SP, Kendigh SC (1938) Variations in the weight of birds. *Auk* 55:416-467
- Barnard CJ, Sibly RM (1981) Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Anim Behav* 29:543-550
- Blem CR (1976) Patterns of lipid storage and utilization in birds. *Am Zool* 16:671-684
- Brittingham MC, Temple SA (1988) Impacts of supplemental feeding on survival rates of black-capped chickadees. *Ecology* 69:581-589
- Caraco T (1979) Time budgeting and group size: a test of theory. *Ecology* 60:618-627
- Czikeli H (1983) Agonistic interactions within a winter flock of slate-colored juncos (*Junco hyemalis*): evidence for the dominants' strategy. *Z Tierpsychol* 61:61-88
- Dawson WR, Marsh RL (1986) Winter fattening in the American goldfinch and the possible role of temperature in its regulation. *Physiol Zool* 59:357-368
- Dawson WR, Marsh RL, Buttemer WA, Carey C (1983) Seasonal and geographic variation of cold resistance in house finches *Carpodacus mexicanus*. *Physiol Zool* 56:353-369
- Desrochers A, Hannon SJ, Nordin KE (1988) Winter survival and territory acquisition in a northern population of black-capped chickadees. *Auk* 105:727-736
- Draper NR, Smith H (1966) Applied regression analysis. John Wiley, New York
- Fretwell S (1969) Dominance behavior and winter habitat distribution in juncos (*Junco hyemalis*). *Bird-banding* 40:1-25
- Fretwell S (1972) Populations in a seasonal environment. Princeton, New Jersey, Princeton University Press
- Hays WL (1981) Statistics. Holt, Rinehart, and Winston, New York
- Helms CW, Drury WH (1960) Winter and migratory weight and fat field studies on some North American buntings. *Bird-banding* 31:1-40
- Helms CW, Smythe RB (1969) Variation in major body components of the tree sparrow (*Spizella arborea*) sampled within the winter range. *Wilson Bull* 81:280-292
- Helms CW, Aussiker WH, Bower EB, Fretwell SD (1967) A biometric study of the major body components of the slate-colored junco *Junco hyemalis*. *Condor* 69:560-578
- Hogstad O (1987) It is expensive to be dominant. *Auk* 104:333-336
- Jansson C, Ekman J, von Brömssen A (1981) Winter mortality and food supply in tits *Parus* spp. *Oikos* 37:313-322
- Keppel G (1982) Design and analysis. Prentice-Hall, Englewood Cliffs, New Jersey
- Ketterson ED, King JR (1977) Metabolic and behavioral responses to fasting in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). *Physiol Zool* 50:115-129
- Kikkawa J (1980) Winter survival in relation to dominance classes among silvereyes *Zosterops lateralis chlorocephala* of Heron Island, Great Barrier Reef. *Ibis* 122:437-446
- King JR (1972) Adaptive periodic fat storage by birds. *Proc 15th Int Ornithol Congr, The Hague*, pp 200-217
- Kleinbaum DG, Kupper LL (1978) Applied regression analysis and other multivariate methods. Duxbury Press, North Scituate, Massachusetts
- Lima SL (1986) Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* 67:377-385
- Lundberg P (1985) Dominance behaviour, body weight and fat variations, and partial migration in European blackbirds *Turdus merula*. *Behav Ecol Sociobiol* 17:185-189
- Millikan GC, Gaddis P, Pulliam HR (1985) Interspecific dominance and the foraging behavior of juncos. *Anim Behav* 33:428-435
- Nolan V, Ketterson ED (1983) An analysis of body mass, wing length, and visible fat deposits of dark-eyed juncos wintering at different latitudes. *Wilson Bull* 95:603-620
- Odum EP (1949) Weight variations in wintering white-throated sparrows in relation to temperature and migration. *Wilson Bull* 61:3-14
- Odum EP, Perkinson JD (1951) Relation of lipid metabolism to migration in birds: seasonal variation in body lipids of the migratory white-throated sparrow. *Physiol Zool* 24:216-230
- Piper WH (1987) Causes and consequences of social dominance in wintering white-throated sparrows. Ph D dissertation. Univ of N Carolina, Chapel Hill, NC
- Piper WH (1989) Exposure to predators and access to food in wintering white-throated sparrows *Zonotrichia albicollis*. Behaviour (in press)
- Piper WH, Wiley RH (1989a) Correlates of dominance in wintering white-throated sparrows: age, sex, and location. *Anim Behav* 37:298-310
- Piper WH, Wiley RH (1989b) Distinguishing the morphs of the white-throated sparrow in basic plumage. *J Field Ornith* 60:73-83

- Pulliam HR, Mills GS (1977) The use of space by wintering sparrows. *Ecology* 58:1393-1399
- Rogers CM (1987) Predation risk and fasting capacity: do wintering birds maintain optimal body mass? *Ecology* 68:1051-1061
- Schneider KCJ (1984) Dominance, predation and optimal foraging in white-throated sparrow flocks. *Ecology* 65:1820-1827
- Snedecor GW, Cochran WG (1967) *Statistical methods*. Iowa State Univ Press, Ames, Iowa
- Stuebe MM, Ketterson ED (1982) A study of fasting in tree sparrows (*Spizella arborea*) and dark-eyed juncos (*Junco hyemalis*): ecological implications. *Auk* 99:299-308
- Vander Wall SB, Balda RP (1981) Ecology and evolution of food-storage behavior in conifer-seed-caching corvids. *Z Tierpsychol* 56:217-242
- Waite TA (1987) Vigilance in the white-breasted nuthatch: effects of dominance and sociality. *Auk* 104:429-434
- Wiedenmann RN, Rabenold KN (1987) The effects of social dominance between two subspecies of dark-eyed juncos, *Junco hyemalis*. *Anim Behav* 35:856-864
- Wingfield JC, Farner DS (1976) Avian endocrinology: field investigations and methods. *Condor* 78:570-573
- Wolfson A (1954) Weight and fat deposition in relation to spring migration in transient white-throated sparrows. *Auk* 71:413-434
- Zach R, Falls JB (1976) Influence of capturing a prey on subsequent search in the ovenbird (Aves: Parulidae). *Can J Zool* 55:1958-1969