Lack of association between allozymic variation and social dominance in free-living White-throated Sparrows

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This study examined possible associations between allozymic variation in metabolic enzymes and social dominance or survival in a large free-living population of wintering White-throated Sparrows (*Zonotrichia albicollis*). Electrophoresis of 15 enzymes resolved from muscle biopsies from 173 sparrows revealed nine enzymes with some variation. Two of these (*PGM* and *6-PGD*) showed substantial variation, with the frequency of the common allele below 0.9. During two seasons dominance interactions among the biopsied birds were observed at three feeding stations. There was no association between social dominance (percentage of opponents dominated) and genotype at the two most variable loci or overall proportion of heterozygotes at either the two most variable loci or the seven most consistently scored loci. Older birds were more likely than expected to be heterozygous at both the *PGM* and *6-PGD* loci, but heterozygotes did not return more frequently than homozygotes in subsequent years. Although we cannot exclude a weak association of dominance and isozyme variability, we can conclude that social dominance during winter lacks any strong relationship with variation at loci for metabolic enzymes.

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On trouvera ici les résultats d'une étude sur les associations possibles entre la variation allozymique des enzymes du métabolisme et la dominance sociale ou la survie chez une grande population naturelle de Bruants à gorge blanche (*Zonotrichia albicollis*) en hiver. L'électrophorèse de 15 enzymes obtenus par biopsie musculaire chez 173 bruants a révélé la présence de 9 enzymes variables. Deux d'entre eux (*PGM* et *6-PGD*) étaient très variables et la fréquence de l'allèle le plus commun était inférieure à 0,9. Les interactions de dominance ont été observées chez les oiseaux opérés à trois points d'alimentation durant deux saisons. Il n'y avait pas de relation entre la dominance sociale (pourcentage d'adversaires dominés) et le génotype aux deux locus les plus variables, ni entre la dominance et la proportion globale d'hétérozygotes aux deux locus les plus variables ou aux sept locus les plus communs. Les oiseaux les plus âgés avaient plus tendance que prévu à être hétérozygotes aux locus *PGM* et *6-PGD*, mais les hétérozygotes n'étaient pas plus fréquents que les homozygotes au cours des années subséquentes. Bien qu'il ne soit pas possible de nier l'existence d'une faible association entre la dominance et la variabilité des isoenzymes, la dominance sociale en hiver n'est pas fortement reliée à la variation enregistrée aux différents locus.

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Introduction

The genetic basis of complex social behavior is not well understood. Several studies, however, have found associations between genetic variation and some types of social behavior. In free-living and captive Dark-eyed Juncos (*Junco hyemalis*), Baker and Fox (1978) reported an association between social dominance and heterozygosity at a single metabolic enzyme locus. Similarly, in a study of captive old field mice, *Peromyscus polionotus*, Garten (1976) found a link between heterozygosity and aggression. These findings suggest that if social dominance or aggression contributes to increased fitness in these species, genetic variation in metabolic enzymes might result in part from heterozygote advantage at loci for metabolic enzymes or at strongly linked loci. Recently, however, Zink and Watt (1987) found no association between heterozygosity for any of the variable allozymes they resolved (including the locus important in Baker and Fox's (1978) study) and social dominance in captive groups of juncos. They also found no association between genetic variation and social dominance in captive groups of Harris' Sparrows (*Zonotrichia querula*) and White-crowned Sparrows (*Zonotrichia leucophrys*). The differences in the results of these studies and the use of captive groups of birds leave the possible general relationship between genetic variation and social dominance in free-living birds uncertain.

Research on the possible links between allozymic variation and social dominance is aided by specific hypotheses regarding a mechanism by which genetic variation at a particular enzyme locus might influence the expression of behavior. Heterozygosity could contribute to general vigor, growth, or developmental homeostasis (Lerner 1959). Such effects have been reported for several organisms other than birds (reviewed by Mitton and Grant 1984), although these effects are often small (see Foltz et al. 1983). In addition, a particular locus might either have a direct influence on behavior or be linked to other loci that directly affect behavior. However, there are few cases in which there is a full mechanistic understanding of the genetic influence on fitness (Koehn and Hilbish 1987).

Associations between genetic variability and social dominance may arise through the action of a third variable. For instance, if heterozygotes have higher survival (through processes other than social dominance), and older birds tend to dominate younger ones, then heterozygosity would appear to be associated with social dominance. Alternatively, variance from unknown correlates of social dominance might mask the effects of genetic variability.

We examined genetic variation in relation to social dominance in a large population of free-living White-throated Sparrows (*Zonotrichia albicollis*). The population under study has been the subject of a long-term investigation of social dominance in wintering birds (Piper 1987; Piper and Wiley 1989*a*, 1989*b*). Social dominance in White-throated Sparrows depends not only on the age and sex of each bird, but also on the location of interactions in the bird's home range. Consequently, we examined the association between dominance and genotype

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while taking into account the age, sex, social history, and location of encounters for each bird.

The White-throated Sparrow is of further interest because of the well-known genetic polymorphism in plumage, which is associated with behavioral and ecological variation among birds in the breeding season (Lowther 1961; Thorneycroft 1966, 1975; Lowther and Falls 1968; Knapton and Falls 1982, 1983; Knapton et al. 1984). The two morphs, which can be identified correctly more than 95% of the time in the breeding (alternate) plumage, can also be distinguished with nearly 90% accuracy in the winter (basic) plumage (Piper and Wiley 1989a). Thus, this species already provides a well-documented case of an association between genetic and behavioral variation in natural populations. It seemed reasonable, therefore, to investigate whether allozymic variation might be associated with morph as well.

Methods

Study area and population

This research was conducted on White-throated Sparrows wintering at the Mason Farm Biological Reserve in Chapel Hill, North Carolina. This population has been the focus of a study of dominance and movement patterns since 1982 (see Piper 1987; Piper and Wiley 1989b). During November–April in 1982–1983 and 1983–1984 we captured and color-banded approximately 400 White-throated Sparrows along a 400-m hedgerow of multiflora rose (*Rosa multiflora*) and blackberry (*Rubus argutus*). In 1982–1983, 10 sites with three to seven treadle traps each were spaced approximately 40 m apart in a line. In 1983–1984 the trapline was expanded to 16 trap locations, 25 m apart, each with a six-celled treadle trap. When first captured, a bird was color-banded, weighed, checked for skull pneumatization, sexed by laparotomy, measured for wing chord length, and scored for crown brightness. The bird was then returned to the site of capture and released.

Previously unbanded birds captured on or before 31 December with fully pneumatized skulls were considered to be at least 1 year old, whereas any bird with an incompletely pneumatized skull was considered to be in its first winter (Piper and Wiley 1989b).

Crown brightness was measured by the procedure described by Piper and Wiley (1989a). Briefly, an index of crown brightness was generated by summing scores for extent of white or black in the median and lateral stripes. Morph was determined in two ways. Approximately half of the birds remained on the study area after their prealternate molt in March and April. These birds were assigned to white or tan morphs by inspection of their alternate plumage. For the remaining birds, morph was determined by means of a formula based on the age and sex of the bird, and the brightness of the median and lateral stripes in the winter plumage. This formula correctly identifies morph in 89% of birds in the population at Mason Farm.

Regular trapping throughout the season resulted in banding of nearly all the birds wintering in the study area. Birds ($N = 250$) were retrapped, on average, 12.1 ($\pm$ 11.7 (SD)) times in a winter. These repeated captures indicated the locations of the birds' home ranges and provided data on each bird's movements throughout the season. White-throated Sparrows on our study area tended to be trapped at only two or three adjacent locations throughout a winter (Piper 1987; Piper and Wiley 1989b). The mean trapping location of each bird was used as an index of the center of the bird's home range and was calculated only for birds captured three or more times during a winter. The standard deviation of the distance from the mean trapping location for a particular bird was used as an index of the bird's tendency to move.

Observations of interactions

We recorded dominance interactions between color-banded sparrows from blinds at three feeding stations 50–100 m apart along the trapline during December–March. At each station small amounts of millet and sunflower seed were provided for the birds at locations within 1.4 m of the hedgerow.

Dominance interactions of similar species have been described by

Sabine (1949) and Balph (1977). We considered all interactions (supplantations, attacks, pursuits, and fights) to be equally indicative of the dominance relationship in a dyad (pair of birds). In 93% of the relationships ($N = 355$), the first interaction observed for a dyad correctly reflected the eventual relationship (Piper and Wiley 1989b). Therefore, we considered one interaction sufficient to allow the relationship between two birds to be assessed. For all dyads, we defined as dominant the bird winning 75% or more of the interactions in the dyad. Dyads in which neither bird dominated the other in 75% or more of the interactions were considered to be undefined and were omitted.

A bird's dominating ability was then calculated as the number of dyads in which the bird was dominant divided by the total number of defined dyads in which it participated. This index, termed the dominance proportion (d), was calculated only for birds with 10 or more defined dyadic relationships and was normalized using the logit transformation $\ln[(d)/(1 - d)]$ (Snedecor and Cochran 1967). The dominance proportion of all biopsied birds included interactions with unbiopsied opponents.

Electrophoresis

We recaptured 98 individuals in March 1983 and 75 in March 1984 and removed small samples of the pectoralis muscle. The exact procedure for these biopsies is described by Westneat (1986). The muscle samples were placed in Tris–HCl buffer, pH 7.4 (Selander et al. 1971), and frozen on dry ice until analyzed.

Electrophoresis was performed at the University of North Carolina a few months later, using standard techniques (Shaw and Prasad 1970; Selander et al. 1971; Harris and Hopkinson 1976; Avise et al. 1980a, 1980b; Zink 1982). We screened 15 loci known to be polymorphic in many species of small passerines (Barrowclough and Corbin 1978; Avise et al. 1980a, 1980b; Zink 1982). Gel, buffer, and running conditions for the polymorphic loci were nearly identical with those used by Westneat (1987). We scored samples by measuring the relative mobilities of each band without knowledge of the identity of the samples.

Analysis

Sample sizes varied between analyses because we did not obtain complete information on a bird's genotype at every locus. In addition, few birds captured in 1982–1983 had sufficient interactions to allow their dominance proportion to be calculated. Unless these birds returned the following year and were observed frequently, they were not included in the analyses of dominance and genotype. Finally, some birds could not be unambiguously scored for age and morph, so these were also excluded from the relevant analyses.

All statistical procedures were performed by SYSTAT (Systat Inc., Evanston, IL). In all tests, the a priori significance level was $p < 0.05$. Associations between variables for categorical data are expressed as the likelihood ratio, G. Correlations between other variables are expressed as the Pearson product–moment correlation coefficient, r.

Results

Genetics

In 1983, we could resolve only eight loci, and five of these showed some variation (Table 1). In 1984, we screened a total of 15 loci and found 9 that exhibited some variation. However, one, adenosine deaminase, could not be scored consistently. In addition, isocitrate dehydrogenase (*IDH*), was resolved midway through the electrophoretic analysis and so many of the birds were not scored for this locus. Most of the loci that were polymorphic showed little variation, with the frequency of the common allele greater than 0.95 and with one or two rare alleles (Table 1). However, the frequency of the common allele was below 0.9 for two loci, phosphoglucomutase (*PGM*) and 6-phosphogluconate dehydrogenase (*6-PGD*). Genotypic frequencies for these two loci fit the frequencies expected for Hardy–Weinberg combinations of allelic frequencies in both

TABLE 1. Allelic frequencies and relative mobilities for the seven polymorphic loci found in White-throated Sparrows

Locus and allele	Mobility	Allelic frequency	
		1982–1983	1983–1984
PGM			
1	60	0.350	0.376
2	100	0.650	0.606
3	130	0.000	0.018
6-PGD			
1	50	0.020	0.012
2	70	0.170	0.171
3	100	0.780	0.812
4	125	0.030	0.006
MPI			
1	90	0.014	0.018
2	100	0.963	0.941
3	104	0.023	0.035
4	107	0.000	0.006
α-GPD			
1	74	0.004	0.024
2	100	0.981	0.971
3	130	0.004	0.006
IDH			
1	100	0.996	0.981
2	200	0.004	0.019
PGI			
1	100	—	0.959
2	180	—	0.007
3	220	—	0.034
PEPT B			
1	70	—	0.027
2	100	—	0.966
3	130	—	0.007
PEPT C			
1	90	—	0.014
2	100	—	0.972
3	114	—	0.014

NOTE: MPI, mannose phosphate isomerase; α-GPD, glycerophosphate dehydrogenase; PGI, phosphoglucose isomerase; PEPT B, peptidase B; PEPT C, peptidase C.
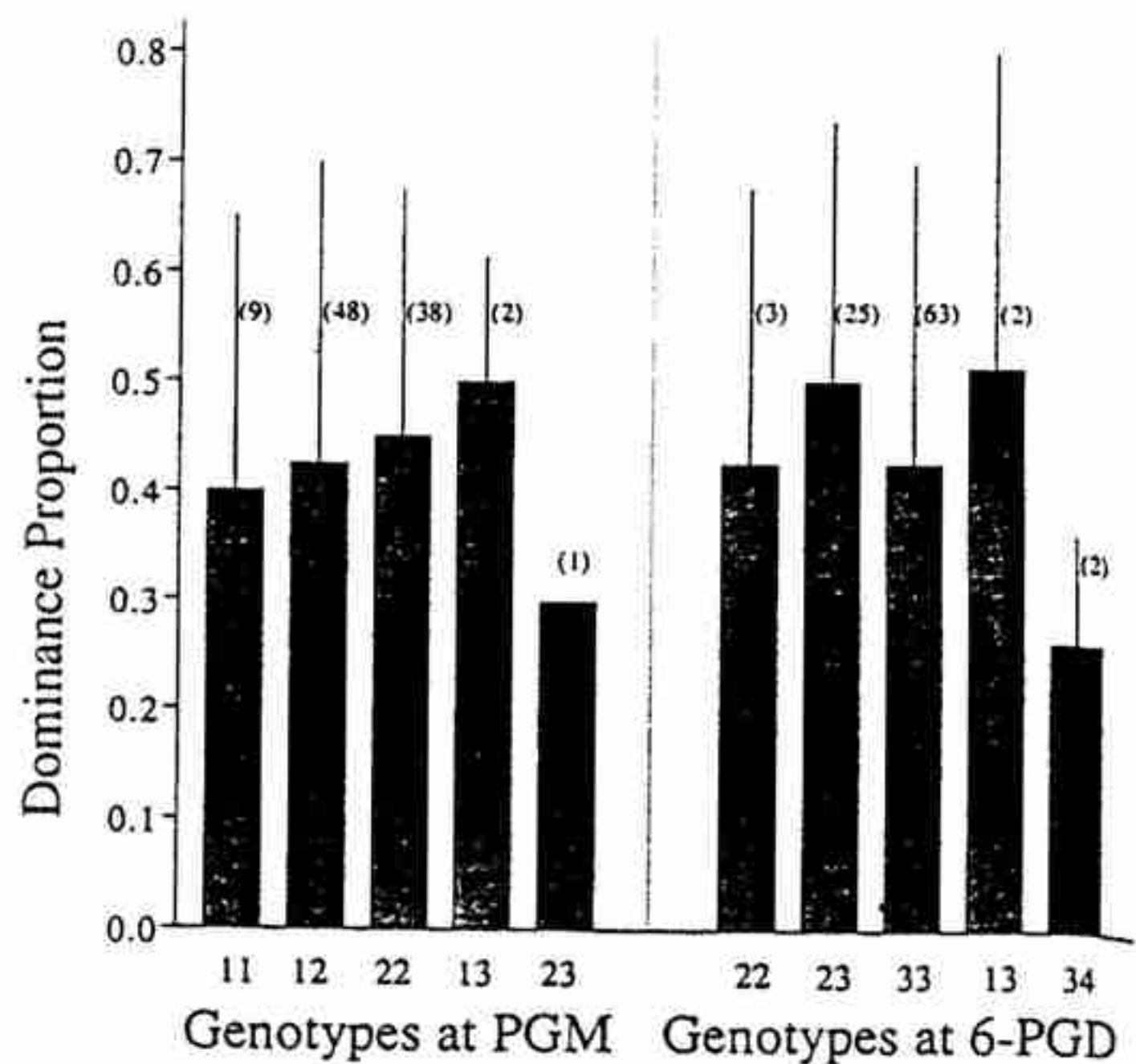

FIG. 1. Average dominance proportion for each genotype at the two most polymorphic loci in wintering White-throated Sparrows. Statistical tests were performed on logit transformations of these data (see text). Vertical bars indicate standard deviation. Numbers in parentheses are sample sizes.

years (1983: PGM, $G = 1.00$, df = 1, $p > 0.2$; 6-PGD, $G = 6.05$, df = 8, $p > 0.5$; 1984: PGM, $G = 1.71$, df = 4, $p > 0.7$; 6-PGD, $G = 1.14$, df = 3, $p > 0.7$). Heterozygotes at all loci also exhibited the banding patterns expected, given the known subunit structure of each enzyme (Harris and Hopkinson 1976). Thus, we concluded that the variation in banding patterns represented genetic variation.

Dominance and genotype

The logit transformation of dominance proportion did not vary among the three most common genotypes at either of the two most variable loci (Fig. 1; one-way ANOVA; PGM, $F_{[2,92]} = 0.04$, $p > 0.9$; 6-PGD, $F_{[2,88]} = 1.29$, $p > 0.2$). In an analysis of the relationship between heterozygosity and dominance, heterozygotes at each of the two most variable loci did not have higher transformed dominance proportions than homozygotes (PGM, $t = 0.26$, df = 96, $p > 0.7$; 6-PGD, $t = 1.44$, df = 94, $p > 0.1$).

Because these results failed to reject the null hypothesis of no effect of heterozygosity, we calculated the power of the statistical test to quantify confidence in accepting the null hypothesis. Assuming an actual difference of 10% in dominance proportion between homozygotes and heterozygotes and the same overall mean, our tests of the association between heterozygosity and dominance for both loci had a probability of 0.53 of rejecting the null hypothesis of no difference (Hays 1981). This result suggests that small (relative to Baker and Fox's (1978) study), but possibly important, effects of heterozygosity on dominance status might have gone undetected by our tests.

We also tested for effects on dominance across several loci, on the assumption that heterozygosity acted additively. There was no correlation between the proportion of loci that were heterozygous and transformed dominance proportion for the two most variable loci together ($r = 0.126$, $F_{[1,93]} = 1.48$, $p > 0.2$), or for total heterozygosity over all seven most frequently resolved loci ($r = 0.032$, $F_{[1,61]} = 0.07$, $p > 0.7$).

Correlates with dominance rank

Dominance in White-throated Sparrows was strongly correlated with distance from mean trapping location, rank in the bird's first year, age, and sex (Piper and Wiley 1989b). We tested the effect of genotype on each of these variables plus arrival date and years of residence separately for the PGM and 6-PGD loci. No particular genotype was associated with the extent of a bird's movements (PGM, $F_{[2,79]} = 2.05$, $p > 0.1$; 6-PGD, $F_{[2,79]} = 0.63$, $p > 0.5$), a bird's rank in its first winter (PGM, $F_{[2,57]} = 1.28$, $p > 0.2$; 6-PGD, $F_{[2,52]} = 0.01$, $p > 0.9$), age (PGM, $G = 6.26$, df = 4, $p > 0.1$; 6-PGD, $G = 5.68$, df = 4, $p > 0.1$), sex (PGM, $G = 0.72$, df = 2, $p > 0.5$; 6-PGD, $G = 0.62$, df = 2, $p > 0.5$), the number of years a bird was resident (PGM, $G = 2.98$, df = 2, $p > 0.1$; 6-PGD, $G = 0.20$, df = 2, $p > 0.9$), or arrival date (PGM, $F_{[2,152]} = 1.13$, $p > 0.3$; 6-PGD, $F_{[2,123]} = 0.28$, $p > 0.7$).

To test the possible additive effects of heterozygosity at each locus and social dominance, we repeated the multivariate

TABLE 2. Variables associated with social dominance in a multivariate analysis

	Variable	p	Overall r
Model with rank in 1st year and two-locus measure ($N = 46$)	Distance from mean trapping location	0.000	
	Rank in 1st year	0.000	
	Age	0.000	
	Sex	0.035	
	Arrival date	0.105	
	H	0.053	
			0.914
Model with rank in 1st year and seven-locus measure ($N = 39$)	Distance from mean trapping location	0.002	
	Rank in 1st year	0.000	
	Age	0.000	
	Sex	0.051	
	Arrival date	0.259	
	H	0.514	
			0.941
Model with two-locus measure ($N = 74$)	Distance from mean trapping location	0.000	
	Sex	0.001	
	Arrival date	0.012	
	Age	0.034	
	Residence (yr)	0.043	
	H	0.506	
			0.784
Model with seven-locus measure ($N = 63$)	Distance from mean trapping location	0.000	
	Sex	0.002	
	Arrival date	0.035	
	Age	0.160	
	Residence (yr)	0.038	
	H	0.458	
			0.748

NOTE: Four models were tested: two included the rank of a bird in its 1st year and two did not. Two measures of heterozygosity (H) were tested: the proportions of loci heterozygous at either the two most variable loci or the seven most frequently resolved loci. N, number of cases.

analysis described by Piper and Wiley (1989b), with the inclusion of two measures of genetic variability, the proportions of loci heterozygous at the two most polymorphic loci and at all seven most frequently resolved loci. Briefly, each analysis consisted of a stepwise multiple regression on all possible variables, with a criterion of $p = 0.15$ to accept each successive variable. We then tested the overall model with all variables chosen by the stepwise procedure and including our measures of genetic variability (see Piper and Wiley 1989b for details). Neither measure of heterozygosity predicted dominance proportion in the multivariate model. Furthermore, including these measures had little effect on the variables that did correlate with dominance rank (see Table 2 for correlates and their p values).

Morph

In this population there is no relationship between morph and dominance (Piper and Wiley 1989b). However, because morph is a chromosomal polymorphism, we tested for a possible relationship between morph and genotype at each of the two most polymorphic loci. No genotype was confined exclusively to one morph, nor was there any statistical relationship with morph at the two loci (PGM, $G = 0.72$, df = 2, $p > 0.5$; $6\text{-}PGD$, $G = 0.12$, df = 2, $p > 0.9$).

Rate of return

We tested for a relationship between the rate of return to the

study area and allozymic variability. No particular genotype at the two most variable loci returned more frequently than expected by chance (PGM, $G = 1.46$, df = 2, $p > 0.3$; $6\text{-}PGD$, $G = 4.16$, df = 2, $p > 0.1$). The proportion of individuals that were heterozygous at the two most variable loci and returned the next year was slightly, but not significantly, lower than expected (both loci heterozygous, rate = 0.21, $N = 24$; one locus heterozygous, rate = 0.32, $N = 63$; both loci homozygous, rate = 0.33, $N = 45$; $G = 1.38$, df = 2, $p > 0.3$). We must caution that although we had a large sample size ($N = 132$), small but important effects of heterozygosity on return rate may have gone undetected by our tests. The lower return rate for heterozygotes is not consistent with an apparent relationship between the two-locus measure of heterozygosity and age ($G = 13.51$, df = 4, $p < 0.01$). However, given the large number of tests performed in the search for correlates with heterozygosity, it is perhaps not surprising to find one such inconsistent result.

Discussion

Our results provide no evidence that either overall genetic heterozygosity or any particular genotype had an association with social dominance or survival of White-throated Sparrows. Consequently, we have found no evidence that social behavior

during winter mediates the action of natural selection on genetic variability at the loci surveyed.

Some of our results suggest indirectly that selection might affect variability at the loci we examined. In particular, the association between the age of a bird and heterozygosity at the two most variable loci might result from selection on these genotypes during the breeding season. However, if genotypes differed in survival during the breeding season but not during the winter, we would expect to find differences in the rates of return of these genotypes. We found no such relationship; in fact, the trend was in the opposite direction. Temporal variation in selection, in particular selection against homozygotes before our study began, could have produced a preponderance of heterozygotes in older age-classes without any association between heterozygosity and survival during our study. We must caution, however, that because of the number of statistical tests performed in the search for possible correlates, one such significant result is likely by chance alone. Thus, we conclude that there is no consistent evidence that selection has operated on these genotypes at any time during the annual cycle.

On the other hand, our results should not be taken as strong evidence that the variability we observed was selectively neutral, as suggested for other avian populations by Barrowclough et al. (1985). Several considerations limit confidence in interpreting our data in that way. Foremost, although our sample of free-living birds was larger than those in previous studies, calculations of the power of our statistical tests indicate that our samples were still insufficient to allow potentially important relationships with heterozygosity to be detected. The strongest conclusion justified by our results is that heterozygosity is not a *major* correlate of social dominance. In this population of wintering sparrows, dominance is most strongly related to location, age, sex, and dominance during the first winter of life (Piper and Wiley 1989b).

Our sample sizes were also not large enough for testing more than a few simple hypotheses about possible associations between genotype and social dominance. In addition to possible heterotic interactions, the alleles at a locus could influence fitness additively or multiplicatively, or could show dominance. We did not attempt to test all these possibilities against the null hypothesis of the neutrality of genetic variation.

Some of the genetic variation among individuals in our population might have resulted from mixing of different breeding populations during migration. In some cases, mixing of separate populations produces a deficit of heterozygotes (Wahlund 1928; Selander et al. 1971). The loci assayed in this study fit expectations of Hardy–Weinberg equilibria, although important deviations might not have been detected statistically. Nevertheless, the sparrows at Mason Farm probably do not belong to any single breeding population. We have had no reports of our banded birds from their breeding grounds, but in another study, White-throated Sparrows banded at one location in South Carolina were subsequently recovered from widely separated locations in the breeding range (Wharton 1941). Mixing of individuals from many different breeding locales with different selective pressures might have produced some of the observed variation.

The birds in our study were not removed from their natural social groups and confined in aviaries. Our study therefore had the advantage of providing a direct examination of the sources and consequences of natural selection, including movement patterns and natural return rates. However, our population was not completely undisturbed. Aside from handling the birds at

intervals throughout the winter, we also provided supplemental food in the form of bait for traps and observation sites. Birds that frequently fed at the observation platforms did have slightly more fat deposits than those that fed less frequently (Piper 1987). However, food was not provided constantly, and the birds' behavior by the end of the winter indicated that they experienced much greater hunger than earlier, when natural food sources were presumably still plentiful. Our provision of supplemental food probably reduced, but did not eliminate, natural selection from competition for food during late winter. The biopsies at the end of each season did not have an effect on the survival or behavior of birds in subsequent winters (Westneat 1986).

The conclusion that social dominance and survival in White-throated Sparrows is not strongly influenced by observed variation at several protein-coding loci is not surprising, as Zink and Watt (1987) discuss. It is unlikely that a complex behavioral trait such as social dominance would be either influenced directly or linked in some way to a few loci for metabolic enzymes. However, we have yet to eliminate the possibility that weak selection has acted to maintain the observed genetic variation at these loci. Because several previous studies have suggested relationships between behavior and genetic variation (Garten 1976; Baker and Fox 1978), we encourage more research on large samples of free-living individuals for the purpose of investigating the factors, genetic and demographic, affecting social dominance.

Acknowledgements

AVISE, J. C., PATTON, J. C., and AQUADRO, C. F. 1980a. Evolutionary genetics of birds. I. Relationships among North American thrushes and allies. Auk, 97: 135–147.
——— 1980b. Evolutionary genetics of birds. II. Conservative protein evolution in North American sparrows and relatives. Syst. Zool. 29: 323–334.
BAKER, M. C., and FOX, S. F. 1978. Dominance. survival. and enzyme polymorphism in dark-eyed juncos. *Junco hyemalis*. Evolution, 32: 697–711.
BALPH, M. H. 1977. Winter social behavior of dark-eyed juncos: communication, social organization, and ecological implications. Anim. Behav. 25: 859–884.
BARROWCLOUGH, G. F., and CORBIN, K. W. 1978. Genetic variation and differentiation in the Parulidae. Auk, 95: 691–702.
BARROWCLOUGH, G. F., JOHNSON, N. K., and ZINK, R. M. 1985. On the nature of genic variation in birds. *In* Current ornithology. Vol. 2. *Edited by* R. F. Johnston, Plenum Press, New York. pp. 135–154.
FOLTZ, D. W., NEWKIRK, G. F., and ZOUROS, E. 1983. Genetics of growth rate in the American oyster: absence of interactions among enzyme loci. Aquaculture, 33: 157–165.
GARTEN, C. T., JR. 1976. Relationship between aggressive behavior and genic heterozygosity in the old field mouse. *Peromyscus polionotus*. Evolution, 30: 59–72.
HARRIS, H., and HOPKINSON, D. A. 1976. Handbook of enzyme

electrophoresis in human genetics. North-Holland Publishing Co., Amsterdam.

HAYS, W. L. 1981. Statistics. 3rd. ed. Holt, Rinehart, and Winston, New York.

KNAPTON, R. W., and FALLS, J. B. 1982. Polymorphism in the White-throated Sparrow: habitat occupancy and nest-site selection. Can. J. Zool. 60: 452–459.

—— 1983. Differences in parental contribution among pair types in the polymorphic White-throated Sparrow. Can. J. Zool. 61: 1288–1292.

KNAPTON, R. W., CARTER, R. V., and FALLS, J. B. 1984. A comparison of breeding ecology and reproductive success between morphs of the White-throated Sparrow. Wilson Bull. 96: 60–71.

KOEHN, R. K., and HILBISH, T. J. 1987. The adaptive importance of genetic variation. Am. Sci. 75: 134–141.

LERNER, I. M. 1959. Genetic homeostasis. John Wiley and Sons, New York.

LOWTHER, J. K. 1961. Polymorphism in the white-throated sparrow, Zonotrichia albicollis (Gmelin). Can. J. Zool. 39: 281–292.

LOWTHER, J. K., and FALLS, J. B. 1968. White-throated Sparrow. In Life histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows, and allies. Edited by O. L. Austin. U.S. Natl. Mus. Bull. No. 237: 1364–1392.

MITTON, J. B., and GRANT, M. C. 1984. Associations among protein heterozygosity, growth rate, and developmental homeostasis. Annu. Rev. Ecol. Syst. 15: 479–499.

PIPER, W. H. 1987. Causes and consequences of social dominance in wintering white-throated sparrows. Ph. D. dissertation, University of North Carolina, Chapel Hill.

PIPER, W. H., and WILEY, R. H. 1989a. Distinguishing morphs of the white-throated sparrow in basic plumage. J. Field Ornithol. 60: 73–83.

—— 1989b. Correlates of dominance in wintering white-throated sparrows: age, sex and location. Anim. Behav. 37: 298–310.

SABINE, W. S. 1949. Dominance in winter flocks of juncos and tree sparrows. Physiol. Zool. 22: 64–85.

SELANDER, R. K., SMITH, M. H., YANG, S. Y., JOHNSON, W. E., and GENTRY, J. E. 1971. Biochemical polymorphism and systematics in the genus Peromyscus. I. Variation in the old field mouse (Peromyscus polionotus). Univ. Tex. Publ. No. 7103. pp. 49–90.

SHAW, C. R., and PRASAD, R. 1970. Starch gel electrophoresis of enzymes:- a compilation of recipes. Biochem. Genet. 4: 297–320.

SNEDECOR, G. W., and COCHRAN, W. G. 1967. Statistical methods. Iowa State University Press, Ames.

THORNEYCROFT, H. B. 1966. Chromosomal polymorphism in the white-throated sparrow, Zonotrichia albicollis (Gmelin). Science (Washington D.C.), 154: 1571–1572.

—— 1975. A cytogenetic study of the white-throated sparrow, Zonotrichia albicollis (Gmelin). Evolution, 29: 611–621.

WAHLUND, S. 1928. Zusammensetzung von Populationen und Korrelationserscheinungen vom Standpunkt der Vererbungslehre aus betrachtet. Hereditas, 11: 65–106.

WESTNEAT, D. F. 1986. The effects of muscle biopsy on survival and condition in white-throated sparrows. Wilson Bull. 98: 280–285.

—— 1987. Extra-pair fertilizations in a predominantly monogamous bird: genetic evidence. Anim. Behav. 35: 877–886.

WHARTON, W. P. 1941. Twelve years of banding at Summerville, S.C. Bird-Banding, 12: 137–147.

ZINK, R. M. 1982. Patterns of genic and morphologic variation among sparrows in the genera Zonotrichia, Melospiza, Junco, and Passerella. Auk, 99: 632–649.

ZINK, R. M., and WATT, D. J. 1987. Allozymic correlates of dominance rank in sparrows. Auk, 104: 1–10.