THE AUK
A QUARTERLY JOURNAL OF
ORNITHOLOGY

VOL. 104 JANUARY 1987 NO. 1

ALLOZYMIC CORRELATES OF DOMINANCE RANK IN SPARROWS

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ABSTRACT.—We tested for associations between allozyme variation and behavioral rank in a dominance hierarchy in White-crowned (*Zonotrichia leucophrys*) and Harris' (*Z. querula*) sparrows and Dark-eyed Juncos (*Junco hyemalis*). Individuals were ranked in species-specific dominance hierarchies by scoring aggressive encounters in an aviary as win/loss interactions. Starch-gel electrophoresis of 42 protein-coding loci established each individual's genotype at each locus; heterozygosity estimates were calculated from the observed genotypes. To test the hypothesis that protein polymorphisms are predictive of an individual's behavioral rank, we compared behavioral rank and measures of heterozygosity and particular genotypes. Neither heterozygosity nor an individual bird's (single or multilocus) genotype was predictive of its rank in the behavioral hierarchy. An individual's sex and age were predictive of dominance rank, with males and adults generally dominant to females and young, respectively. Our data seem to conflict with those of Baker and Fox (1978), who reported that individual Dark-eyed Juncos that were heterozygous at a peptidase locus (also surveyed by us) were relatively more dominant than homozygous individuals. As a null hypothesis, we suggest that genetic variation at allozyme loci does not influence behavior.
Received 15 October 1985, accepted 12 June 1986.

ELECTROPHORETIC analysis of protein variation has led to a reasonably detailed description of genetic variation in natural populations of a wide variety of organisms (Nevo 1978, Avise and Aquadro 1982, Smith et al. 1982). Many authors have discussed the maintenance of genetic variation and its evolutionary or adaptive significance (e.g. Lewontin 1974, Kimura 1983, Koehn et al. 1983, Nevo et al. 1984). In a growing body of literature (see Zouros and Foltz in press) investigators report on empirical tests for associations between levels and patterns of genetic variation (heterozygosity and genotypes, respectively) at protein-coding loci and the expression of various phenotypic traits, such as morphological variance (Eanes 1978, McAndrew et al. 1982, Chakraborty and Ryman 1983, Fleischer et al. 1983, Zink et al. 1985), growth rate (Koehn and Shumway 1982, Ledig et al. 1983, Garton et al. 1984, Mitton and Grant 1984, Mitton and Koehn 1985), developmental stability (Kat 1982, Leary et al. 1983, Ferguson 1986), and behavior (Garten 1976, Baker and Fox 1978). A theoretical basis for adaptive interpretations of correlations between heterozygosity and phenotypic traits derives in part from Lerner's (1954) hypothesis of genetic homeostasis. For example, increased levels of heterozygosity might buffer or canalize the phenotype from environmental perturbations during development, resulting in decreased morphological variance. The assumption that follows is that the phenotype obtained is optimally adaptive and confers a fitness advan-

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tage to individuals possessing that phenotypic state. Orzack (1985) develops a contrasting viewpoint. In another scenario, heterozygous individuals might be biochemically or physiologically more efficient (a "positive energy balance"), which would allow them to channel more energy into activities such as growth (Garton et al. 1984, Mitton and Koehn 1985) or behavioral interactions.

In view of potential associations between enzyme heterozygosity and fitness traits, one can envision how natural selection might influence both the adaptive expression of a fitness trait and the maintenance of enzyme polymorphisms. Several models predict an association between genes that encode enzymes surveyed electrophoretically and genes that influence the fitness trait (Zouros and Foltz 1984, in press). Linkage disequilibrium could produce an association between either allozyme genotypes or heterozygosity for protein-coding loci and loci coding for other traits. Loci surveyed electrophoretically might contribute genetic variation directly in the particular metabolic pathways that influence particular traits (Mitton and Grant 1984). The hypothesis of associative overdominance also predicts a significant correlation between variation in the two sets of loci (Thomson 1977, Zouros and Foltz in press). Thus, empirical documentation and analysis of the association (direct or indirect) between enzyme polymorphisms and the expression of fitness traits might clarify the genetic basis of adaptation in such traits, and identify a mechanism for the adaptive maintenance of enzyme polymorphisms. Resolution of the nature of selection at allozyme loci is of importance because of the consistency with selective neutrality obtained by Barrowclough et al. (1985) for a broad sampling of avian taxa.

Baker and Fox (1978) reported that Dark-eyed Juncos (*Junco hyemalis*) that were heterozygous ("AB") at a peptidase locus (leucylglycyl-glycine, Lgg) were of relatively high dominance rank in wintering flocks. Birds of higher dominance rank could realize enhanced fitness because of increased survival. Hence, there is potentially an association between dominance (survival/nonsurvival) and the maintenance of genetic variation at Lgg, via one of the pathways discussed above. In this study, we compared dominance rank and genotype at 42 presumptive genetic loci in the White-crowned Sparrow (*Zonotrichia leucophrys*), Harris' Sparrow (*Z. querula*), and Dark-eyed Junco. We found that neither genotype(s) at allozyme loci nor genic heterozygosity were predictive of behavioral dominance rankings.

MATERIALS AND METHODS

Specimens.—All individuals were captured with mist nets during fall migration, winter, or early spring migration. Sex was determined by inspection of gonads, and age was determined by the degree of skull ossification when possible. Birds with unossified areas in the skull, indicating that the individual was hatched during the prior breeding season, were denoted as "HY" (hatching year), whereas individuals with completely ossified skulls were classified as adults over one year of age ("AHY," after hatching year). For birds captured in fall or late winter, but not killed until spring, we did not determine age.

White-crowned and Harris' sparrows were captured near Norman, Oklahoma (Cleveland Co.), during November 1980 and maintained at the Behavior Laboratory, University of Oklahoma. Dark-eyed Juncos were captured at Notre Dame, Indiana (St. Joseph Co.), in February or March 1983 and maintained at Saint Mary's College. All three species were housed and tested under similar conditions in aviaries (approximately 3 m on a side), fed a game bird chow/seed mixture, and exposed to short daylength using automatic lighting simulating natural winter light periods. All birds were color banded for individual recognition. Dominance relationships were determined (see below) for 14 Harris' Sparrows (mixed ages), 11 White-crowned Sparrows (mixed ages), and 9 White-crowned Sparrows (AHY birds only) at Norman during December 1980. Dominance behaviors for a group of 24 Dark-eyed Juncos were assessed in April 1983, and for a group of 30 (different) Dark-eyed Juncos in May 1983, at Notre Dame. Specimens were preserved as study skins or skeletons and housed at the American Museum of Natural History (New York) or Saint Mary's College. Samples of frozen tissue are stored at the Museum of Vertebrate Zoology, University of California, Berkeley, California.

Behavior.—Each group of birds was housed in a test aviary and observed through a one-way window overlooking a shelf on which food and water were placed. Surplus food and water were removed during daily 2–3-h observation periods. Observations of a flock were often continued for several days. Interactions were recorded as win/loss encounters between two identified birds, and included aggressive encounters (attacks, dominant bird flying at or pecking the other bird) and avoidances (subordinate bird dodging, running away from the dominant bird). All such encounters were tabulated into a matrix for each group and arranged to minimize nonlinearity following Brown (1975). The resulting ordered matrices were then used to define the linear hierarchy of in-

dividual dominance rankings in each group. Watt (1986) provides additional details of experimental methods.

Electrophoresis.—After behavioral observations were recorded, birds were killed and frozen. Samples of heart, liver, pectoral muscle, and kidney were taken from each specimen and preserved at −76°C. Preparation of tissue extracts and electrophoretic conditions followed Zink (1982, in press). Acronyms for loci were those used by Harris and Hopkinson (1976), and protein and enzyme assays followed Selander et al. (1971) and Harris and Hopkinson (1976). The genotype of each individual at each locus was inferred from the banding pattern on the gel. Individual locus banding patterns conformed to those predicted based on the subunit structure reported for other vertebrates (e.g. Harris and Hopkinson 1976, Avise et al. 1980). Therefore, we refer to electrophoretic variants, or electromorphs, as alleles. The most common allele at a locus was denoted by an "M," and alleles with more cathodal or anodal migrations were coded as "S" or "F," respectively. Pluses and minuses were used to designate additional alleles with different electrophoretic mobilities. Individual heterozygosity (h) was calculated by dividing the number of loci at which an individual was heterozygous by the total number of loci scored (42).

Statistical analysis.—Several possibilities exist for comparing dominance rank, genotype, and heterozygosity. We used h as an indication of a bird's level of genetic variation, and compared rankings of h and dominance. We recognize that an individual with four heterozygous loci is not necessarily more "genetically variable" than an individual with one or two such loci, especially if interlocus variance in heterozygosity exists (Chakraborty 1981). Level of heterozygosity at a few loci surveyed electrophoretically could be related to variation in other traits if the two sets of loci (one for h estimate, one for trait under study) are in linkage disequilibrium, or if allozyme loci directly influence a trait (Mitton and Grant 1984). Therefore, we compared h with behavioral rank. Heterozygosity might be a better measure of genetic variability if averaged over individuals and loci (H), and then compared between independent groups of individuals (i.e. demes; see Nei 1978). Thus, for our two hierarchies of juncos, we calculated H for each consecutive group of six birds to document levels of heterozygosity throughout the hierarchy. Comparison of H-values may not be optimal (Archie 1985) because, for example, the independence of these groups of six from a wintering sample is uncertain.

To compare genotypes with dominance rank we assessed whether or not individuals with a particular genotype (single or multilocus) occurred in a particular region of the hierarchy more often than expected by chance. The junco hierarchies were divided into halves, and a G-test (contingency table; Sokal and Rohlf 1981) was performed on the proportions of Lgg heterozygotes, following Baker and Fox (1978).

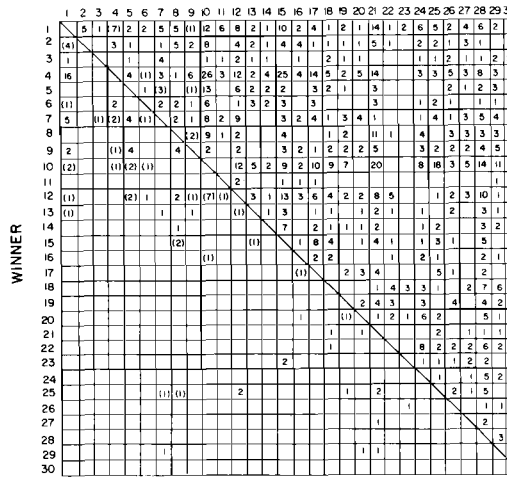

Fig. 1. Matrix of win/loss encounters among 30 Dark-eyed Juncos. Numbers in parentheses indicate reversals, wins by birds that were shown to be subordinate in most encounters involving that bird. Arrangement of win/loss encounters in a matrix such as this, minimizing values below the diagonal, allowed the linear ranking (in Appendix 5) of individuals in order of dominance, with bird 1 being the most dominant (see Brown 1975).

Results

Nonallozymic correlates of dominance rank.—Observed win/loss encounters for one group of juncos were arranged in order of dominance (Fig. 1). Matrices for the other junco group, as well as the Harris' and White-crowned sparrow groups, are available from the second author. Males of all three species tended to dominate females (Appendices 1-5), and AHY birds tended to dominate HY birds in the fall groups (Appendices 1-3).

Genetic variation and dominance rank.—Forty-two presumptive genetic loci were scored for each individual of all three species. The relative dominance rank, h, and genotype for variable loci for the Harris' Sparrow are indicated in Appendix 1. There was no tendency at any locus for birds of a given genotype to be dominant or subordinate. Also, by inspection, dominance rank and h were not meaningfully associated. For example, individuals of each heterozygosity "class" occurred throughout the hierarchy and were not clustered in any one region. The same results were obtained for the two groups of White-crowned Sparrows (Appendices 2 and 3), namely that single-locus ge-

notypes and h were not predictive of dominance rank.

Inspection of the dominance hierarchies for juncos failed to reveal an association between genotype(s) and dominance rank (Appendices 4 and 5). Because of Baker and Fox's (1978) results, we confirmed statistically a lack of heterogeneity in the proportions of heterozygous genotypes at Lgg in the top and bottom halves of each of the two hierarchies of juncos (Appendix 4, $G = 0.17$; Appendix 5, $G = 0.14$; for each and both combined, $P > 0.05$). Contrasting the total number of heterozygous genotypes in the top and bottom halves of each hierarchy revealed no heterogeneity. In Appendix 4 there are 18 heterozygous genotypes in both the top and bottom halves of the hierarchy, whereas in Appendix 5 there are 25 in the top and 27 in the bottom half.

In both junco hierarchies, the average heterozygosity of groups of six individuals did not vary in a predictable manner with rank in the hierarchy. In fact, the highest H-value (5.2%) occurred in the bottom half (most subordinate birds) of a hierarchy (Appendix 5). A search for individuals with the same multilocus genotype revealed 27 different multilocus genotypes among the 30 individual Dark-eyed Juncos (Appendix 5); the 3 individuals with the same multilocus genotype are scattered throughout the hierarchy. A similar result was obtained for the other four hierarchies analyzed.

DISCUSSION

Neither allozyme genotypes (single or multilocus) nor heterozygosity were predictive of behavioral status in White-crowned and Harris' sparrows and Dark-eyed Juncos. Dominance rank in these species is related to age and sex but not to genetic polymorphisms at protein-coding loci. Generally, male sparrows are larger than females, and this probably contributes to their ability to dominate females. Older (AHY) birds might dominate first-year (HY) birds in fall samples because of greater experience in food-related contests. Thus, large, older males were generally the most dominant.

Several biases could inhibit our finding an association between heterozygosity or genotype and dominance rank. For example, Foltz et al. (1983) found that heterozygosity at enzyme loci explained about 4% of the variance in growth rate in oysters. Therefore, if the heterozygosity-fitness trait association is a weak one, sample sizes larger than those used in the present analysis might be needed to detect it. We note, however, that an association has been observed in studies (e.g. Baker and Fox 1978) with sample sizes similar to ours. Thus, we acknowledge that a weak association might exist, the biological significance of which would be unknown. Our results were consistent for five independent aviaries and three species. We suggest that our results point to a general lack of an association between variation at enzyme loci and behavioral dominance.

The independence of allozymic variation and dominance rank is not necessarily unexpected. It would seem improbable to discover by chance an enzyme genotype, such as AB at Lgg, that was either directly or indirectly associated with a genetically complex trait such as dominance.

Also in need of consideration is the relationship between heterozygosity at enzyme loci and variation in other parts of the genome. Heterozygosity estimates based on a few enzyme loci are unlikely to be representative, for individuals or populations, of heterozygosity either genome-wide or in a subset thereof, such as a "behavioral pathway" (Nei 1978, Chakraborty 1981, Turelli and Ginzburg 1983). Hence, in theory it is equivocal whether birds with higher relative heterozygosity at allozyme loci are also more heterozygous for genes that influence behavior. In practice, no empirical associations were detected here between dominance and genetic variation at enzyme loci in three species of emberizid finches. Thus, we assume that genes that influence behavior are independent of those we surveyed electrophoretically. Phenotypic traits that are associated significantly with heterozygosity (Zouros and Foltz in press) may be those such as growth rate (Koehn and Shumway 1982) that are influenced in a more direct manner by loci coding for proteins and metabolic enzymes than are traits such as behavioral dominance.

Our study was prompted by Baker and Fox's (1978) report that dominance status and survival in wintering Dark-eyed Juncos was significantly associated with a particular genotype at Lgg (heterozygous, AB). Their results are significant because they suggest that fitness is correlated with a particular genotype at an enzyme locus, which has an unknown contribution to the genetic basis of behavioral dominance. Also, their results imply that natural selection can affect enzyme polymor-

phisms because of an association between genes that encode enzymes surveyed electrophoretically and those that influence behavior. Although our studies conflict, neither study need be wrong, as selection pressures and environmental conditions could differ between sites and years. Also, the two studies employed different experimental designs. Baker and Fox (1978) biopsied individuals and introduced birds of known genotype into their aviaries. Below, we explore empirical and theoretical aspects of the two studies to identify sources of conflict.

Baker and Fox surveyed 18 presumptive genetic loci, 6 of which were found to be polymorphic, but concentrated on the most polymorphic one, Lgg; they detected 3 alleles (A', A, B) and 4 (A'A, AA, AB, BB) of the 6 possible genotypes. Genotypic proportions did not differ significantly from Hardy-Weinberg expectations; hence, the wintering population shows signs of being outbred. Baker and Fox noted microgeographic and seasonal variation. In particular, AB genotypes tended to be more frequent late in the season at a site for which samples were obtained throughout the season. Although the effect was not significant statistically, Baker and Fox suggested that selection might be favoring heterozygotes. For individuals in each of two free-ranging flocks of juncos, Baker and Fox ranked individuals in terms of dominance, divided each of the two resultant dominance hierarchies in half, and determined that a significantly higher number of AB (vs. A'A, AA, BB) individuals occurred in the top half of the 1974–1975 hierarchy, but not in 1975–1976.

We observed five alleles at Lgg, and based on similar frequencies our F, M, and S alleles probably correspond to the A', A, and B alleles in Baker and Fox's study. There is little geographic differentiation in allozymes among most conspecific avian populations (Barrowclough 1983), a result that extends to at least western North American populations of the Dark-eyed Junco (Barrowclough pers. comm.). We think that overall levels (heterozygosity) and patterns of genetic variation at Lgg are comparable between our samples and those of Baker and Fox, even though the samples were taken 1,000 km and 8–10 years apart. Time, geographic distance, and genotypic differences between samples are unlikely to account for the conflicting results of our studies. We were impressed with what seems to be temporal stability in genotypic proportions, a result potentially inconsistent with a fitness advantage for heterozygotes.

The genetic mechanism by which individuals heterozygous at a peptidase locus are more dominant and exhibit enhanced survival is difficult to detect. Because dominance and survival are probably genetically complex traits (Turelli 1984), the protein products of the Lgg locus are unlikely to exert a direct detectable physiological influence on behavior. Heterosis was mentioned (tentatively) by Baker and Fox as a potential genetic mechanism. Baker and Fox pooled A'A genotypes with AA and BB, which confounds testing the effect of heterozygosity per se at Lgg. Because we were interested in the effect of heterozygosity at the Lgg locus, we calculated *G*-values for both of their 1974–1975 and 1975–1976 groups, contrasting heterozygous (AB and A'A) and homozygous (AA and BB) genotypes; neither value was significant (1974–1975, $G = 3.45$; 1975–1976, $G = 0.03$; for both, $P > 0.05$). Therefore, the AB genotype must be special, and not heterozygosity at Lgg. That is, there could be a heterotic effect only when the A and B alleles are combined in an individual. The A and B alleles each could be linked to different sets of "behavioral genes," making AB birds superior competitors in food-related contests owing to the combination (heterosis) of the two suites of behavioral genes. In this case, AB at Lgg would be a marker. The hypothesis of associative overdominance (Zouros and Foltz in press) offers a somewhat similar theoretical justification.

Tests for consistency with linkage disequilibrium or heterozygote advantage are possible. Selection against homozygotes (both at Lgg and "behavioral loci") over the course of winter should have resulted in a relatively high proportion of heterozygotes in our samples from late winter/early spring; this was not observed. If only AB individuals survived by winter's end, genotype proportions observed the following fall when birds arrive on wintering sites might not differ from expectations, because genotypic proportions would return to Hardy-Weinberg equilibrium at each breeding season. Each autumn, genotypic proportions would be dependent on the relative abundance of adults (all heterozygotes) and immatures. In our data there were no differences between adults and immatures in h or genotypic char-

acteristics. No departures from Hardy-Weinberg expectations were detected either in this study or in that of Baker and Fox. However, detecting minor departures statistically is difficult. Heterozygote advantage would lead to allelic frequencies of 0.50, a result that was not observed in either study. Of course, if the two homozygous classes have different, nonzero fitnesses that are less than the AB genotype, almost any gene frequencies could result. Thus, although it is useful to describe the necessary genetic model and its predictions, it is difficult to establish the significance of an association between Lgg genotype and dominance rank.

A potential reconciliation between the results of Baker and Fox (1978) and ours could obtain if there were a relationship between age and heterozygosity. For example, in some organisms, adult survival is related to heterozygosity, such that older individuals tend to be more heterozygous (Zouros and Foltz in press). Although we have no data to test for such an effect in sparrows, dominance or competitive ability in our aviary experiments could be an age-dependent phenomenon. If the adults in Baker and Fox's aviaries tended to be older (and more heterozygous) than those in our analyses, we might have failed to confirm the relationship predicted from Baker and Fox's results.

Baker and Fox (1978) also tested for correlates among dominance rank, Lgg genotype, and survival. Four groups of birds of known genotypes were used to contrast AB vs. AA and BB individuals where "survival" was measured as maintenance of body mass above 17 g, nonsurvivors being those birds that dropped to 17 g. This scheme could introduce a statistical bias against female survivorship (Ketterson and Nolan 1983), which would be problematic if there is a tendency for one sex to be disproportionately represented by heterozygotes. We examined the effect of genotype on survival in relation to the potentially confounding influence of sex. The data are numbers (males/females) of genotypes and survivorship: heterozygous survivors (20/1) and nonsurvivors (8/4), and homozygous survivors (15/4) and nonsurvivors (17/12). We used a three-way ($2 \times 2 \times 2$) log-linear partial association test (Sokal and Rohlf 1981) on the pooled data of Figs. 2 and 3 of Baker and Fox. Male domination of females produced a significant sex × survivorship effect ($G = 5.94$, $df = 1$, $P < 0.05$), as noted by Baker and Fox. The other two-way effects were insignificant: sex × genotype effect ($G = 1.75$, $df = 1$, $P > 0.05$), and genotype × survival ($G = 2.79$, $df = 1$, $P > 0.05$). Therefore, holding sex constant, the significance of genotype on survival was not supported. We suggest that whether heterozygotes at Lgg realized enhanced survivorship is equivocal.

Baker and Fox's results for the 1974–1975 hierarchy suggest a relationship between genotype and dominance rank, an effect we failed to replicate. Their important study deserves continued attention via further tests for associations between enzyme variation and fitness traits, such as behavioral dominance. These future studies should consider both theoretical and empirical design, and appropriate genetic models. An adaptive association between behavior and genetic variation at enzyme loci remains a viable possibility. Fleischer et al. (1983) suggested that morphological variance was significantly correlated with enzyme heterozygosity in House Sparrows (*Passer domesticus*), although Handford (1980) and Zink et al. (1985) failed to find such an association. In our opinion, a null hypothesis that enzyme polymorphisms are maintained by stochastic processes (i.e. selective neutrality) should be excluded before adaptive interpretation of associations between enzyme polymorphisms and behavioral dominance (see Gould and Lewontin 1979, Schnell and Selander 1981). Evidence supports the hypothesis that most enzyme polymorphisms are selectively neutral in 23 of 24 avian populations tested (Barrowclough et al. 1985).

ACKNOWLEDGMENTS

This study was financed in part by NSF grant DEB-7920694 (to N. K. Johnson), by the Frank M. Chapman Memorial Fund, and by a Faculty Research Grant to the second author by Saint Mary's College. We are grateful to these sources. G. F. Barrowclough, N. K. Johnson, and A. Larson contributed important ideas to this project. M. C. Baker and S. F. Fox provided assistance with analytical procedures in their paper. G. F. Barrowclough, J. A. Gerwin, M. S. Hafner, E. D. Ketterson, S. M. Lanyon, R. Ostfeld, D. P. Pashley, J. V. Remsen, G. D. Schnell, and D. B. Wake made helpful comments on the manuscript. D. W. Foltz, F. J. Rohlf, and F. J. Sonleitner provided statistical advice.

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APPENDIX 1. Behavioral rank, sex, age, and genotype at the 5 polymorphic loci in 14 Harris' Sparrows. Blanks for genotypes indicate homozygosity for the common allele (e.g. MM). Codes for alleles: M = medium mobility, F = fast relative to M, and S = slow relative to M. Pluses and minuses code further allelic states. For sex, M = male and F = female. For age, AHY = after hatching year, and HY = hatching year.

Rank	Sex	Age	6-Pgd	Icd	Gpi	Pgm	Ada	No. of heterozygous loci
1	M	AHY	MS					1
2	M	AHY	MS			MS		2
3	?	AHY						0
4	F	AHY	MS^-					1
5	F	AHY	MS^-	FM			FM	3
6	F	AHY				MS		1
7	F	AHY						0
8	F	HY			FM			1
9	F	HY	MS					1
10	F	HY					FM	1
11	F	HY						0
12	F	HY	MS					1
13	F	HY		FM				1
14	F	HY		FM	FM			2

APPENDIX 2. Behavioral rank, sex, age, and genotype at the 12 polymorphic loci in 11 White-crowned Sparrows. Abbreviations are defined in Appendix 1.

	Rank										
	1	2	3	4	5	6	7	8	9	10	11
Sex	M	M	M	M	F	M	F	?	F	F	M
Age	AHY	AHY	AHY	AHY	AHY	HY	HY	HY	HY	HY	HY
Lgg			MS								
La1						FM					
La2											FM
Icd								FM			
Gpi									FM		
Ada			FM				FS			FM	FM
6-Pgd	MS	MS			MS	MS					
Np							FM				
Acp							FM				
Est					MS						
Adh	FM										
Gsr		FM		FM	FM				FM	FM	
No. of heterozygous loci	2	2	2	1	3	2	3	1	2	2	2

APPENDIX 3. Dominance rank, sex, age, and genotype at the 8 polymorphic loci in 9 White-crowned Sparrows. Abbreviations are defined in Appendix 1.

	Rank								
	1	2	3	4	5	6	7	8	9
Sex	M	M	F	M	M	M	M	M	M
Age	AHY	AHY	AHY	AHY	AHY	AHY	AHY	AHY	AHY
Lgg	MS	MS				MS			
Icd									FM
Gpi									FM
Ada						FM			
6-Pgd			MS	MS	MS			MS	
Est			MS						
Adh								FM	
Gsr		FM	FM	FM			FM		FM
No. of heterozygous loci	1	2	3	2	1	2	1	2	3

APPENDIX 4. Dominance rank, sex, and genotype at the 12 polymorphic loci in Dark-eyed Juncos. The average heterozygosities for groups of 6 birds, starting with birds 1–6, are 0.032, 0.040, 0.032, and 0.040, respectively. Abbreviations are defined in Appendix 1.

Rank	Sex	Lgg	Acon	6-Pgd	La1	La2	Icd	Ada	Ck	Eap	Pt2	αGpd1	αGpd2	No. of heterozygous loci
1	M								FM					1
2	M											MS		1
3	M	SS	MS				FM							2
4	M	FM												1
5	M					MS								1
6	M							MS			MS			2
7	M	FS						FM						2
8	M	MS				SS					MS			2
9	M							F+M						1
10	M	MS												1
11	M	MS						MS		FM		MS		4
12	M	SS												0
13	M	MS	MS			SS		FM						3
14	M	SS												0
15	M	MS		MS				MS						3
16	M													0
17	M			FM										1
18	M	MS												1
19	M	MS												1
20	F									FM			MS	2
21	F				MS									1
22	F	FM				MS								2
23	F	SS											FM	1
24	F	FM		MS									MS	3

APPENDIX 5. Dominance rank, sex, and genotype at the 15 polymorphic loci in 30 Dark-eyed Juncos. For the following loci, only one bird is heterozygous: La1 (22 FM), Est (18 MS), Pgm (9 MS), Icd (25 FM), Gsr (27 MS), and Mdh (15 FM). The average heterozygosities for each group of 6, starting with birds 1–6, are 0.044, 0.040, 0.040, 0.032, and 0.052, respectively. Abbreviations are defined in Appendix 1.

Rank	Sex	Lgg	Acon	Gpi	6-Pgd	La2	Np	Ada	αGpd1	αGpd2	No. of heterozygous loci
1	M									MS	1
2	M		FM								1
3	M	MS					FM	FM			3
4	M	FM	MS								2
5	M	FM	FF								1
6	M	FM				MS			MS		3
7	M	MS			MS		FM			MS	4
8	M				MS						1
9	M				MS			FM			3
10	M	SS									0
11	M				MS						1
12	M	FM									1
13	M	SS						MS-			1
14	M							MS			1
15	F	F+M									2
16	F	FS			MS						2
17	F							FM			1
18	F	MS						MS			3
19	M								MS		1
20	F	SS				MS					1
21	F	MS			FM			FM			3
22	F				MS						2
23	F				MS						1
24	F										0
25	F	SS		FM		MS	FM				4
26	F							MS			1
27	F	MS						FM			3
28	F			MS					MS		2
29	F	MS			MS						2
30	F	MS-									1