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RELATIONSHIPS BETWEEN GENETIC VARIATION AND BODY SIZE IN WINTERING MALLARDS

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ABSTRACT.—Mallards (*Anas platyrhynchos; n* = 282) wintering in the Southern High Plains (SHP) of Texas were collected from 15 October 1988 to 7 February 1989. Lipid and fat-free body masses were determined for all Mallards. Birds were surveyed electrophoretically for genetic variation at 30 biochemical loci. Our objective was to determine if structural size, fat mass, or fat-free mass of Mallards were related to multilocus genetic variation. Wing-chord length, our estimator of structural size in Mallards, was shortest in female Mallards with the highest levels of genetic variation. Fat mass and fat-free mass of Mallards (corrected for size) were not related to multilocus heterozygosity. Mixtures of morphologically and genetically differentiated breeding populations of Mallards on the SHP wintering area may explain the relationships between multilocus heterozygosity and size we detected in these birds. *Received 6 June 1994, accepted 27 January 1995.*

THE IMPORTANCE OF carcass reserves and body size to survival and reproductive success is well documented for many waterfowl species (Haramis et al. 1986, Hohman 1986, Conroy et al. 1989, Ankney et al. 1991, Gloutney and Clark 1991). For instance, survival probabilities are positively related to large body mass in Canvasbacks (*Aythya valisineria*; Haramis et al. 1986) and Black Ducks (*Anas rubripes*) with condition indices above the median have higher survival rates than those below the median (Conroy et al. 1989). Mallards in good condition (body mass/wing length) have higher survival rates (Bergan 1990) and lower band-recovery rates (Hepp at al. 1986) than birds in poor condition, and Mallards with large lipid reserves have greater probabilities of surviving periods of severe weather stress than those with low lipid stores (Whyte 1983).

Few data currently exist pertaining to the role of genetic variation in maintenance of carcass reserves or determination of body size in waterfowl species. Rhodes and Smith (1993) detected weak relationships between carcass component levels and multilocus heterozygosity in American Wigeons (*A. americana*) wintering in the Southern High Plains region. Furthermore, Rhodes and Smith (1993) indicated that the interpretation of these relationships was confounded by samples that included mixtures of birds from different breeding populations with potentially different genetic characteristics (Rhodes et al. 1993). Studies of the Lesser Snow Goose (*Chen caerulescens caerulescens*; Davies et al. 1988) and the Barnacle Goose (*Branta leucopsis*; Larsson and Forslund 1992) indicate that genetic as well as environmental factors contribute significantly to heritability of body size in these species. In addition, a study by Rhymer (1992) suggested that environmental factors contributed more to interpopulation differences in growth and morphology of Mallards than did genetics.

Data for invertebrate and vertebrate species provide correlative evidence of relationships between genetic variation and protein mass (Rodhouse and Gaffney 1984), lipid reserves (Cothran et al. 1987), and metabolic efficiency (Teska et al. 1990). Genetic variation at the single-locus or multilocus level has been correlated to functional characteristics that are important to fitness in a number of species (Allendorf and Leary 1986). Survival of Blue Grouse (*Dendragapus obscurus*; Redfield 1974), territory size of Willow Ptarmigan (*Lagopus lagopus*; Rorvik et al. 1990), reproductive success of Rock Doves (*Columbia livia*; Frelinger 1972), and survival of Dark-eyed Juncos (*Junco hyemais*; Baker and Fox 1978) have been correlated with genetic char-

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acteristics. Correlations between genetic characteristics and secondary productivity may stem from relationships between genetic variation and metabolic efficiency (Mitton and Grant 1984, Teska et al. 1990). It is important to determine whether genetic diversity explains a significant proportion of the variation in characteristics such as body size or fat mass of waterfowl species. Increased understanding of the relationships between genetic variation and fitness-related characteristics of waterfowl might lead to the use of genetic data for interpretation of survival potentials, reproductive rates, breeding strategies, or movement patterns.

The Mallard is one of the most studied waterfowl species in North America (Bellrose 1980), but relationships between genetic variation and critical characteristics such as lipid mass, body size, or protein mass have not been investigated. The winter portion of the annual cycle of Mallards may often be energetically demanding, especially in the SHP of Texas (Whyte 1983, Whyte et al. 1986). The ability of Mallards to store and use lipid and protein reserves is critical to their overwinter survival (Owen and Cook 1977, Bergan 1990). An assessment of relationships between genetic variation and characteristics related to survival, performed during the overwinter period in the SHP, should provide valuable insights into the biology of Mallards and baseline data in this relatively unexplored area of waterfowl genetics.

Our objectives were to evaluate relationships between multilocus genetic variation and body fat mass or fat-free body mass of wintering Mallards. Based on past examinations of these types of relationships in vertebrate species, our *a priori* predictions were that significant correlations between genetic variability and characteristics related to survival would exist for Mallards.

METHODS

Mallards ($n = 282$) were collected in the SHP region of Texas from 15 October 1988 through 7 February 1989. Sex and age were determined for each bird based on cloacal and feather characteristics (Carney 1981). Body mass (g) and the mass of the omental fat deposit (g) were measured for each Mallard. Wing-chord length (cm; WL) also was recorded for each bird. Samples of liver and muscle tissue were taken and frozen at −70°C for electrophoretic analysis.

Fat mass (g) was estimated for each bird using the equation:

$$\text{total fat mass} = 60.2 + (8.06)(\text{omental fat [g]}), \quad (1)$$

which was derived by Whyte and Bolen (1984; $r^2 = 0.81$) using data collected on Mallards ($n = 624$) from the SHP over a three-year period. Fat-free body mass was estimated for each bird as total body mass minus estimated fat mass. WL was used to remove the effects of structural size in analyses involving fat mass and fat-free body mass. This approach for size correction of dependent variables is similar to that described in Hanson et al. (1990). Fat mass and fat-free body mass values were regressed against WL (separately for each sex and age class) and the resulting residuals were used to calculate new dependent variables corrected for body size. The general equation used to generate these size-corrected variables for each sex and age class was:

$$\text{corrected fat mass or fat-free mass} = \text{residual} + \text{mean fat mass or fat-free mass} \quad (2)$$

(Alisaushas and Ankney 1987, Kehoe et al. 1987). Data for wintering Mallards were assigned to four time periods as in Whyte et al. (1986): autumn (15 October–2 November), early winter (3 November–5 December), midwinter (6 December–7 January), and late winter (8 January–7 February).

Mallards were surveyed for genetic variation at 30 biochemical loci following Rhodes et al. (1991). A diethoritol grinding solution was used with all tissue samples to avoid degradation of the disulfide bonds. Enzymes were stained using various tissue-buffer combinations as follows: liver on amine-citrate (gel pH 6.1/tray pH 6.1)—aspartate aminotransferase 1&2 (AAT), malate dehydrogenase 1&2 (MDH), lactate dehydrogenase 1&2 (LDH), creatine kinase 1&2 (CK), aconitase 1&2 (ACO), α-glycerophosphate dehydrogenase (AGPD), glucose phosphate isomerase (PGI), 6-phosphogluconate dehydrogenase (6-PGD), leucyl alinine peptidase 1&2 (PEP), leucine amino peptidase 1 (LAP), and diaphorase 1&2 (DIA); liver on tris maleate (7.4/7.4)—adenosine deaminase (ADA) and isocitrate dehydrogenase 2 (ICD); liver on tris citrate (8.0/8.0)—iditol dehydrogenase (IDDH), general protein 1 (GP), and albumin (ALB); liver on poulik discontinuous (8.2/8.7)—mannose phosphate isomerase (MPI); muscle on amine citrate (6.1/6.1)—nucleoside phosphorylase (NP), phosphoglucomutase 1 (PGM), and acid phosphotase (ACP); muscle on tris citrate (8.0/8.0)—malic enzyme 1&2 (ME) and isocitrate dehydrogenase 1 (ICD).

Alleles were scored based on their anodal or cathodal position relative to the common allele at each locus. Genotypes marginally scorable at any locus were reanalyzed. If an individual genotype was unresolvable, it was scored as missing (<2% of total). There was no evidence of the presence of null alleles associated with any missing genotypes. For loci with a common allele frequency of less than 0.90, Mallards with heterozygous or rare homozygous genotypes were reanalyzed to confirm their original scoring. Birds were assigned to multilocus heterozygosity classes (H: 0–1, 2, 3, or ≥4) based on their total number

TABLE 1. Main effect ($\bar{x} \pm 1$ SE) presented for dependent variables fat (g; corrected for size), fat-free mass (g; corrected for size), uncorrected fat-free mass (g), and wing-chord length (cm).[a]

	n	Fat	Fat-free mass	Uncorrected fat-free mass	Wing-chord length
			Sex		
Male	185	186.4 ± 5.9^{A}	1,067.3 ± 7.3^{A}	1,066.9 ± 7.4^{A}	29.3 ± 0.1^{A}
Female	97	179.1 ± 9.6^{A}	931.3 ± 11.8^{B}	926.5 ± 12.0^{B}	27.6 ± 0.1^{B}
			Age		
Adult	142	185.3 ± 9.0^{A}	1,032.2 ± 11.1^{A}	1,028.7 ± 11.3^{A}	28.6 ± 0.1^{A}
Juvenile	140	180.2 ± 6.7^{A}	966.4 ± 8.2^{B}	964.6 ± 8.3^{B}	28.2 ± 0.1^{B}
			Season		
Autumn	69	152.1 ± 10.2^{A}	1,042.4 ± 12.5^{A}	1,044.9 ± 12.7^{A}	28.6 ± 0.1^{A}
Early winter	61	190.6 ± 11.0^{B}	990.7 ± 13.5^{B}	984.5 ± 13.7^{B}	28.3 ± 0.1^{A}
Midwinter	82	190.1 ± 10.2^{B}	965.3 ± 12.5^{B}	967.0 ± 12.8^{B}	28.6 ± 0.1^{A}
Late winter	70	198.1 ± 12.6^{B}	998.9 ± 15.5^{B}	990.4 ± 15.8^{B}	28.3 ± 0.2^{A}
			H		
0–1	72	188.2 ± 10.0^{A}	999.7 ± 12.3^{A}	1,003.5 ± 12.5^{A}	28.6 ± 0.1^{A}
2	80	180.4 ± 10.3^{A}	1,003.7 ± 12.6^{A}	999.5 ± 12.8^{A}	28.4 ± 0.1^{AB}
3	67	184.2 ± 10.1^{A}	1,017.9 ± 12.4^{A}	1,023.1 ± 12.7^{A}	28.7 ± 0.1^{A}
≥4	63	178.3 ± 13.5^{A}	975.9 ± 16.6^{A}	960.7 ± 16.9^{B}	28.1 ± 0.2^{B}

[a] Main effect means for each dependent variable are not different if they share same uppercase letter.

of heterozygous loci, and individuals unscored at any single locus were deleted from analyses involving H.

An analysis of variance (ANOVA) was performed to detect differences in WL among Mallards with differing levels of H. ANOVAs also were used to detect differences in fat mass or fat-free body mass (corrected and uncorrected for size) among Mallards in different H classes. Analyses involving fat mass and fat-free body mass were performed both with and without size corrections because a significant relationship between WL (size) and H was detected. Age, sex, season, and the interactions of these variables with H were included in all models. Significance levels for pairwise least-significant-difference comparisons were adjusted for the number of pairwise comparisons performed within each main effect using the Dunn-Sidak multiplicative inequality:

$$1 - (1 - \alpha)^{1/k}, \quad (3)$$

where k is the number of pairwise comparisons in the subset model and α is 0.05 (Sokal and Rohlf 1981). Chi-squared statistics were used to test for differences in the proportions of Mallards of different sexes and ages distributed among multilocus heterozygosity classes. Analyses were performed using the GLM, FREQ, and UNIVARIATE procedures of the Statistical Analysis System (SAS Institute 1989).

RESULTS

The number of alleles per locus ranged from one to nine. Single-locus heterozygosities ranged from 0.00 to 0.50 (Rhodes 1991) and H for Mallards was 0.08 ± SE of 0.03. Fat masses of Mallards varied significantly among seasons. Mallards had lower total fat mass during the autumn period than at any other portion of the winter (Table 1). No differences were detected in mean fat mass (corrected or uncorrected) among H classes, or as a consequence of any interactions involving sex, age, or season and H (Table 2).

WLs of Mallards were different between sex and age classes, and there was a significant interaction between sex and H (Tables 1 and 2). Differences in WL among birds with differing H were not the same for males and females (Fig. 1). In the analysis of fat-free masses, without corrections for size, there were significant differences in fat-free mass between sex and age classes, among seasons, and among H classes of Mallards (Table 2). Male Mallards were heavier than females, adults were heavier than juveniles, and Mallards were heavier in the autumn than in any other portion of the winter (Table 1). Mallards in the highest H class were lighter than all others (Table 1). The interaction terms involving sex and H (Fig. 1) and age, season, and H also were close to significance in the analysis of uncorrected fat-free masses of Mallards (Table 2).

When the data for fat-free masses were corrected for size before analysis, only differences between sex and age classes, and differences

TABLE 2. Degrees of freedom (df) and *F*-values (*P*-values in parentheses) from analyses of variance involving dependent variables fat (g; corrected for size), fat-free mass (g; corrected for size), fat-free mass uncorrected for body size (g), and wing-chord length (cm). Independent variables sex, age, season, and heterozygosity class (*H*) and all two- or three-way interactions involving *H* are presented.

Model	df	Fat	Fat-free mass	Uncorrected fat-free mass	Wing-chord length
Sex	1	0.4 (0.53)	93.8 (<0.01)	96.7 (<0.01)	149.6 (<0.01)
Age	1	0.2 (0.65)	22.4 (<0.01)	20.6 (<0.01)	6.9 (<0.01)
Season	3	3.9 (<0.01)	6.5 (<0.01)	7.0 (<0.01)	1.5 (0.22)
H	3	0.2 (0.93)	1.4 (0.24)	3.0 (<0.03)	3.2 (0.02)
Sex × *H*	3	0.7 (0.56)	1.1 (0.36)	2.3 (0.08)	2.8 (0.04)
Age × *H*	3	1.6 (0.19)	0.1 (0.95)	0.1 (0.99)	0.3 (0.86)
Season × *H*	9	1.0 (0.41)	0.6 (0.83)	1.0 (0.42)	1.7 (0.09)
Sex × Age × *H*	3	0.0 (0.99)	0.2 (0.88)	0.4 (0.74)	0.9 (0.44)
Sex × Season × *H*	9	0.6 (0.76)	0.6 (0.78)	0.7 (0.71)	1.0 (0.41)
Age × Season × *H*	9	0.7 (0.74)	1.7 (0.09)	1.9 (0.06)	1.0 (0.47)

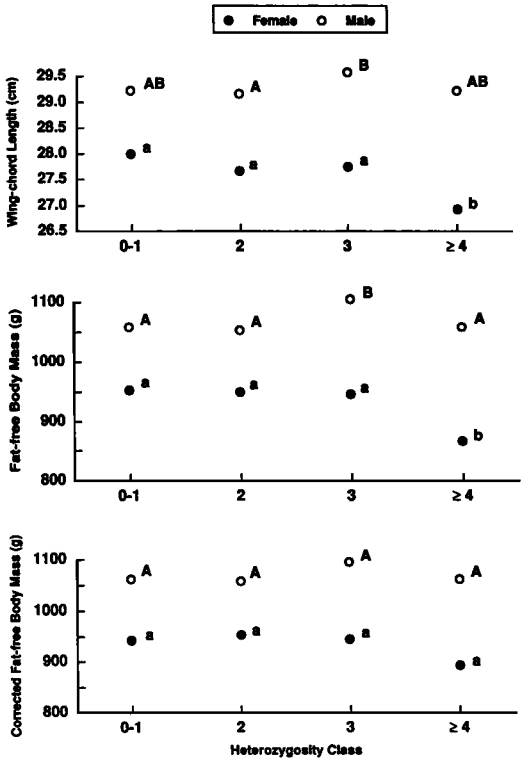

Fig. 1. Wing-chord length (cm), fat-free body mass (g), and fat-free body mass corrected for size (g) for both male and female Mallards, collected on Southern High Plains of Texas during fall and winter of 1988–1989 for each multilocus heterozygosity class (0–1, 2, 3, ≥4). Different uppercase (male) or lowercase (female) letters by plotted means indicate significant differences among heterozygosity classes within each sex.

among seasons remained significant (Tables 1 and 2). Male and adult Mallards were heavier than females and juveniles, respectively and Mallards attained their heaviest fat-free body masses in the autumn period (Table 1). Heterozygosity and interactions involving *H* were no longer important sources of variation in fat-free body mass (Table 1, Fig. 1). Mallards of different sexes and ages were distributed independently with regard to multilocus heterozygosity class ($P = 0.63$).

DISCUSSION

A primary impediment to population genetics research on Mallards and other waterfowl species has been the perception that these species lack the genetic variability necessary for use in correlative and discriminatory examinations (Anderson et al. 1991, Rhodes et al. 1991). Taxonomic studies in which electrophoretic data were used have produced estimates of *H* in Mallards at 4% for 18 loci (Patton and Avise 1985) and at 0.00 for 10 loci (Numachi et al. 1983). In a study of Black Duck and Mallard hybrids, Ankney et al. (1986) estimated *H* at 29 loci for Mallards from California (0.076), Saskatchewan (0.05), Manitoba (0.06), and Ontario (0.05). A descriptive study of genetic variation in Mallards that winter in the SHP region, performed by Parker et al. (1981), estimated *H* at 20 loci to be only 0.027 in this species. Estimates of *H* for Mallards wintering in the SHP region during 1988–1989 (0.08) and 1987–1988 (0.08; Rhodes et al. 1991) are at the high end of the range of

previously published values. These estimates indicate that sufficient genetic diversity is maintained by Mallards to evaluate relationships between H and body size or carcass component proportions in this species.

The most striking result obtained from our analyses was that of the relationship between H and WL (our estimator of size). With and without corrections for size, it is clear that the relationship between H and WL is the driving force behind our results from the analysis of fat-free mass. When fat-free mass was corrected for structural size, all significant heterozygosity effects disappeared. Our *a priori* hypothesis that H would be positively correlated to fat mass or fat-free mass was not supported by these data. Rather, we detected differences in the structural size of Mallards relative to their multilocus heterozygosity.

Assessments of Mallard band returns indicate that birds wintering in the SHP region of Texas originate from at least six major breeding areas, ranging from northwestern to southeastern Canada (Nichols and Hines 1987:85–125). Therefore, the Mallards we collected come from a mixture of breeding-ground populations. In addition, Rhodes et al. (1995) demonstrated that 12% or more of the total genetic variation exhibited by Mallards wintering on the SHP was partitioned among their original breeding populations. The relationships between H and WL detected in these Mallards probably results from the inclusion of birds with different genetic and structural characteristics in the sample. For instance, the smaller sizes of female Mallards in H class ≥ 4 may be a consequence of adaptation to long-term environmental pressures in specific breeding populations. An example of this type of structural differentiation among populations exists for Canada Geese (*Branta canadensis*; Johnsgard 1978), which maintain significant interpopulation morphological differentiation in the presence of gene flow (Raveling 1976).

Natural selection has often been considered the explanation for greater relative fitness in individuals exhibiting specific genetic characteristics (Crow and Kimura 1970, Price and Boag 1987). However, in field studies it is difficult to prove that variation in fitness-related characteristics of individuals is due to selection. Past studies have pointed out the advantages of large body mass to waterfowl during the critical wintering period (Haramis et al. 1986, Bergan 1990), and Kendeigh (1969) noted that there are higher relative metabolic costs experienced by structurally smaller birds.

In the case of female Mallards, the most genetically variable birds exhibited the lowest structural sizes. Maintenance metabolism (Garton et al. 1984), growth and feeding rates (Garton 1984), protein turnover rates (Hawkins et al. 1986), and metabolic efficiency (Teska et al. 1990) have been shown to be positively related to H in a variety of species. Positive relationships between H and metabolic processes may provide mechanisms through which populations of smaller Mallards with high genetic diversity may adapt to specific environmental conditions, just as well as populations with lower heterozygosities and larger body size. However, the hypothesis that populations of Mallards with high genetic diversity and, potentially, greater metabolic efficiency might adapt to become structurally smaller has not been addressed in waterfowl species.

Recent work by Rhymer (1992) suggested that differences in growth, development, and morphological variation among populations of Mallards was primarily attributable to environmental influences. However, significant family effects detected in the analyses performed by Rhymer (1992) indicated a potentially important interaction between genetic and environmental variance within populations. The variance component attributable to the interaction of genetic and environmental factors could not be directly addressed by Rhymer (1992). In light of the evidence for genetic structuring among Mallard populations by Rhodes et al. (1995) and the relationship between WL and H reported in this study, it is likely that the interaction between genetic and environmental factors plays an important role in the determination of structural size in some Mallard populations.

Our data suggest that contributions of genetic and environmental factors to morphological variation in Mallards needs to be reassessed. Metabolic efficiency, maintenance metabolism, and other physiological mechanisms must be compared for Mallards with different genetic characteristics to determine the mechanisms through which the relationships observed in this study were achieved. Genetic surveys of female Mallards from breeding-ground locations both within and among flyways should be performed concurrently to collections of data

on body size and structure to elucidate geographic patterns of genetic and morphological diversity in this species.

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