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RELATIONSHIPS BETWEEN GENETIC VARIATION AND CARCASS COMPONENTS IN WINTERING AMERICAN WIGEONS

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ABSTRACT.—Carcass reserves (fat and protein) were estimated for American Wigeons (*Anas americana*) collected in the Southern High Plains of Texas during 1 October 1988 to 15 March 1989. Wigeons also were surveyed electrophoretically for genetic variation at 25 biochemical loci. Our objective was to determine if nutrient reserves were correlated with multilocus genetic heterozygosity (H). Differences were detected in mean fat, protein and condition values of wigeons with different multilocus genetic characteristics. These differences were confounded by interactions of H, sex, age class, and/or collection period (autumn, early winter, midwinter, late winter, and early spring). The number of American Wigeons in different heterozygosity classes was not independent of sex, season or collection site on the study area. An important implication is that as the genetic structure of wigeon populations changes in time or space relative fitness of those populations may be directly affected. *Received 9 January 1992, accepted 25 August 1992.*

BODY MASS is thought to be related to the survival of individuals in a number of waterfowl species (Haramis et al. 1986, Bergan 1990). In addition, waterfowl often catabolize stored fat or protein reserves during winter (Baldassarre et al. 1986, Whyte et al. 1986, Heitmeyer 1988), and fluctuations in body mass and lipid or protein reserves have been observed in many anatids including Mallards (*Anas platyrhynchos*; Whyte et al. 1986), American Black Ducks (*A. rubripes*; Reinecke et al. 1982), Northern Pintails (*A. acuta*; Smith and Sheeley 1993), and Green-winged Teals (*A. crecca*; Baldassarre et al. 1986). Demographic (sex and age) and climactic factors affect patterns of overwinter change in these nutrient reserves of waterfowl (Bennett and Bolen 1978, Whyte and Bolen 1984).

Wintering waterfowl populations may be comprised of individuals from geographically dispersed breeding ground locations (Bellrose 1980, Nichols and Hines 1987:85-125). Wintering birds that originate from disjunct geographic regions may have undergone different selective environmental pressures during the nonwinter portion of their annual cycle. Natural selection, gene flow, and mating systems interact to determine the genetic and functional characteristics of these geographically disjunct breeding populations (Anderson et al. 1992). Researchers who have investigated factors involved in the dynamics of nutrient reserves in wintering birds have been unable to partition out the variance associated with specific genetic characteristics. In addition, little is known about the influence of genetic variation on nutrient reserves or survival in breeding populations of ducks with different genetic structures (Rhodes et al. 1991).

Examination of the relationships between genetic variation and winter nutrient reserves of American Wigeons could elucidate the role of genetic variability in the maintenance of lipid and protein reserves in this species. Few studies have examined relationships between genetic variation and fitness related characteristics of avian species. The following have been shown to be correlated with genetic variation: survival of Blue Grouse (*Dendragapus obscurus*; Redfield 1973, 1974), Red Grouse (*Lagopus lagopus scoticus*; Henderson 1977), and Dark-eyed Juncos (*Junco hyemalis*; Baker and Fox 1978); reproductive success of Rock Doves (*Columba livia*; Frelinger 1972); and territory size of Willow Ptarmigans (*Lagopus lagopus lagopus*; Rorvik et al. 1990). There also is evidence to suggest that correlations between genetic characteristics and growth/fecundity may be a result of relationships between genetic variation and metabolic efficiency in a number of vertebrate species (Mitton and Grant 1984, Teska et al. 1990).

The objectives of this study were to investigate the relationships of carcass components (protein and fat) and condition of American Wigeons to multilocus heterozygosity. Based on past examinations of these types of relationships in other vertebrate species, our expectations were that significant positive correlations would exist between multilocus heterozygosity and carcass composition of American Wigeons.

METHODS

A total of 618 American Wigeons (289 adult males, 136 juvenile males, 96 adult females, and 97 juvenile females) was collected by shooting in the Southern High Plains region of Texas between 1 October 1988 and 15 March 1989. Sex and age class were determined for each bird on the basis of cloacal and feather characteristics (Carney 1981, Wishart 1981). Wing chord (length, mm from alula to tip of 10th primary), total body length (distance, mm measured from tip of bill to posterior point of pygostyle), and body mass (kg) were recorded for each bird. Wigeons were plucked and samples (2–3 g) of liver and muscle tissues excised from each bird; samples were frozen at −70°C for electrophoretic analysis. The carcass was frozen.

In the laboratory, ingesta were removed from thawed birds, carcass mass (mg) was recorded, and birds were refrozen. Frozen carcasses were sectioned with a meat saw and twice passed through an electric meat grinder. The homogenate was freeze-dried to a constant mass and then reground. Ether-soluble lipid content (fat) of the carcass homogenate was determined using Soxhlet ether extraction of 10- to 20-g samples (16 h). Ash (mineral) content of each bird was determined by combustion of duplicate 3- to 5-g samples of lean dry carcass in a muffle furnace (600°C). When duplicates differed by more than 10%, additional samples were analyzed. Subtraction of water, ash, and fat from carcass mass yielded ash-free lean dry mass (protein), an index of protein (Raveling 1979).

Birds were assigned to five time periods (seasons) during the winter based on the work of Whyte et al. (1986): autumn (1 October–2 November), early winter (3 November–5 December), midwinter (6 December–7 January), late winter (8 January–7 February), and early spring (8 February–15 March). Carcass mass corrected for structural size was estimated as carcass mass divided by the sum of body length and wing length, and the result was termed condition (Wishart 1979).

American Wigeons were surveyed for genetic variation at 25 biochemical loci following Rhodes et al. (1991). A dietheorital grinding solution was used with all tissue samples to avoid degradation of disulfide bonds. Enzymes were stained using various tissue-buffer combinations. Aspartate aminotransferase 1&2 (AAT), malate dehydrogenase 1&2 (MDH), lactate dehydrogenase 1&2 (LDH), aconitase 1 (ACO), a-glycerophosphate dehydrogenase (AGPD), glucose phosphate isomerase (PGI), 6-phosphogluconate dehydrogenase (6-PGD), leucyl alinine peptidase 1&2 (PEP), leucine amino peptidase 1 (LAP), diaphorase 1 (DIA), and menadione reductase (MNR) were scored using liver on amine-citrate (gel pH 6.1/tray 6.1). Adenosine deaminase (ADA) and isocitrate dehydrogenase 2 (ICD) were scored using liver on tris maleate (7.4/7.4). Iditol dehydrogenase (IDDH) was scored using liver on tris citrate (8.0/8.0). Mannose phosphate isomerase (MPI) was scored using liver on Poulik discontinuous (8.2/8.7). Nucleoside phosphorylase (NP), phosphoglucomutase 2 (PGM), and acid phosphotase (ACP) were scored using muscle on amine citrate (6.1/6.1). Malic enzyme 1&2 (ME) and isocitric dehydrogenase 1 (ICD) were scored using muscle on tris citrate (8.0/8.0).

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

Analyses of variance (ANOVA) were used to detect differences in mean fat mass, ash mass, AFLD mass, and condition values among American Wigeons in different H classes. Age, sex, season, and the interactions of these variables with H were included in all models. Age, sex, and season have been shown to explain a significant proportion of the variance in total-body fat mass and body mass in American Wigeons (Rhodes 1991, Wishart 1979). Two- and three-way interactions were reduced into their component parts and conditional main effects were tested within the framework of the full factorial model. All pairwise comparisons were performed within each significant subset model. For instance, all possible pairwise comparisons were performed between seasonal means of birds within an age and H class, if the F-test for differences among seasons was significant in the subset model involving the birds in that age and H class. Significance levels for pairwise least-significant-difference comparisons were adjusted for the number of pairwise comparisons performed within each subset ANOVA using the Dunn-Sidak multiplicative inequality $[1 - (1 - \alpha)^{1/k}]$, where k is the number of pairwise comparisons in the subset model and α is 0.05 (Sokal and Rohlf 1981).

Log-linear models (G-tests) were used to test for differences in the multilocus heterozygosity distributions among sexes, ages, and seasons of wigeons. Birds were assigned to five regions across the study area based on point of collection. Log-linear models also were used to evaluate differences in the multilocus heterozygosity distributions among the regions. Because time and region are confounded, it was not possible to separate those effects.

TABLE 1. Degrees of freedom (df), F-values, and P-values from analyses of variance involving the dependent variables fat, protein, and condition. Independent variables sex, age, season, and heterozygosity class (H), and all two- or three-way interactions significant in at least one model are presented.

		Fat		Protein		Condition	
Model	df	F	P	F	P	F	P
Sex	1	9.5	<0.01	98.7	<0.01	3.4	0.06
Age	1	12.8	<0.01	7.1	<0.01	18.2	<0.01
Season	4	36.5	<0.01	2.7	0.03	12.1	<0.01
H	4	1.3	0.26	0.8	0.51	0.8	0.51
	4	2.3	0.03	2.7	0.03	4.2	<0.01
Age·Season	4	4.6	<0.01	0.6	0.64	4.0	<0.01
H·Season	16	1.2	0.23	1.2	0.24	1.7	0.04
Sex·Age·H	4	2.4	0.05	2.0	0.09	2.2	0.07
Age·Season·H	16	1.9	0.02	0.3	0.99	0.7	0.77
Sex·Season·H	16	0.4	0.98	1.5	0.09	0.7	0.77

Analyses were performed using the GLM and UNIVARIATE procedures of the Statistical Analysis System (SAS Institute 1989), and log-linear models were performed using nonparametric procedures of BMDP (BMDP Statistical Software 1990).

RESULTS

The number of alleles per locus ranged from one to eight. Single-locus heterozygosities ranged from 0.00 to 0.38, with H being 0.08 ± SE of 0.02 (Rhodes 1991). Differences were detected in fat, protein, and condition among birds in different H classes; however, these differences were confounded by interactions among: age, season, and H (for fat); sex, season, and H (for protein); age, sex, and H (for fat, protein and condition); and season and H (for condition; Table 1). No genetic main effects or interactions were detected in analyses involving ash mass.

Differences in fat were detected among birds of different H classes within seasons only for juveniles (Table 2). However, differences in fat among seasons were detected in both adults and juveniles (Table 2). Differences in protein were related to H class, season of collection, and sex (Table 3). Differences in condition values among birds in different H classes were detected only during late winter (Fig 1). Differences also were found for fat, protein and condition between adults and juveniles of each sex, within many H classes, but no differences were detected among H classes within a sex-age class.

The number of American Wigeons in different H classes was not independent of sex and season. This was primarily due to an interaction of H and season (Table 4). There was no differ-

TABLE 2. Mean fat mass (g; $\bar{x} \pm$ SE) for each multilocus heterozygosity class (H) and season combination within each age for American Wigeons collected on Southern High Plains of Texas during fall and winter of 1988–1989.[1]

H	Autumn	Early winter	Midwinter	Late winter	Early spring
			Adults		
0	78.4 ± 8.9^{a}	163.6 ± 18.3^{b}	124.8 ± 9.1^{ab}	103.6 ± 10.6^{a}	101.8 ± 7.9^{a}
1	70.2 ± 8.5^{a}	148.7 ± 9.2^{b}	129.8 ± 7.6^{b}	114.7 ± 9.3^{bc}	84.0 ± 6.8^{ac}
2	78.7 ± 6.2^{a}	163.1 ± 10.2^{b}	128.3 ± 6.4^{bc}	111.5 ± 9.9^{c}	64.2 ± 6.7^{a}
3	100.6 ± 10.4^{a}	160.3 ± 10.4^{b}	105.6 ± 11.8^{a}	118.7 ± 14.3^{ab}	81.4 ± 7.3^{a}
≥4	83.3 ± 10.7^{a}	119.3 ± 16.5^{ab}	150.2 ± 13.5^{b}	121.7 ± 38.8^{ab}	72.8 ± 12.8^{a}
			Juveniles		
0	42.9 ± 9.7^{ABa}	132.9 ± 22.4^{b}	103.8 ± 13.6^{b}	126.7 ± 20.7^{Ab}	91.4 ± 25.1^{ab}
1	88.2 ± 11.1^{Aa}	104.3 ± 22.3^{ab}	144.0 ± 8.7^{b}	115.3 ± 13.5^{ABab}	75.5 ± 6.8^{a}
2	56.9 ± 7.8^{ABa}	123.9 ± 17.6^{ac}	125.5 ± 17.2^{bc}	122.5 ± 7.3^{Ab}	85.2 ± 9.8^{c}
3	35.6 ± 5.6^{Ba}	87.4 ± 21.5^{b}	121.8 ± 16.8^{b}	79.4 ± 15.6^{Bab}	111.8 ± 21.5^{b}
≥4	56.9 ± 18.0^{AB}	109.0 ± 22.4	87.2 ± 23.2	76.4 ± 23.3^{B}	93.9 ± 16.3

[1] Significant differences ($P < 0.05$) in mean fat mass among seasons within an H class and age indicated by different lowercase characters. Those among H classes within a season and age indicated by different uppercase characters.

TABLE 3. Mean protein (g; $\bar{x} \pm$ SE) for each multilocus heterozygosity class (*H*) and season combination within each age for American Wigeons collected on Southern High Plains of Texas during fall and winter of 1988–1989.[1]

H	Autumn	Early winter	Midwinter	Late winter	Early spring
			Males		
0	131.9 ± 5.5^{a}	120.6 ± 2.6^{ABab}	119.4 ± 2.4^{ab}	115.3 ± 2.1^{b}	124.3 ± 2.9^{ab}
1	126.0 ± 6.4	119.0 ± 3.2^{A}	124.1 ± 2.3	117.2 ± 2.5	117.5 ± 2.3
2	121.3 ± 2.3	121.9 ± 3.6^{AB}	122.0 ± 2.2	118.2 ± 2.1	120.1 ± 2.4
3	130.3 ± 3.2	125.3 ± 3.9^{AB}	125.6 ± 4.0	118.4 ± 3.6	124.1 ± 4.1
≥4	125.0 ± 5.3^{ab}	131.7 ± 4.9^{Ba}	125.8 ± 4.9^{ab}	112.0 ± 6.9^{b}	126.5 ± 4.1^{ab}
			Females		
0	98.6 ± 7.2^{AB}	108.8 ± 1.4	126.6 ± 10.9	106.4 ± 7.1	109.4 ± 5.0^{AB}
1	99.6 ± 3.8^{A}	112.2 ± 2.1	108.6 ± 2.1	109.4 ± 3.0	103.0 ± 3.9^{AB}
2	109.5 ± 4.4^{ABab}	116.9 ± 6.2^{a}	105.1 ± 3.3^{ab}	107.8 ± 2.1^{ab}	95.8 ± 3.4^{Ab}
3	108.4 ± 2.3^{AB}	102.4 ± 5.0	111.3 ± 4.2	100.4 ± 4.7	111.6 ± 3.0^{B}
≥4	116.9 ± 10.5^{Ba}	116.8 ± 7.8^{a}	106.7 ± 4.3^{ab}	103.9 ± 3.3^{ab}	87.3 ± 17.8^{Ab}

[1] Significant differences ($P < 0.05$) in mean protein mass among seasons within an *H* class and age indicated by different lowercase characters. Those among *H* classes within a season and age indicated by different uppercase characters.

ence in the number of American Wigeons of different multilocus heterozygosities among sex and age classes, or among age classes within seasons. The number of birds in *H* classes differed among the collection regions.

DISCUSSION

Estimates of *H* for American Wigeons wintering in the Southern High Plains region of Texas during 1988–1989 (0.08) and 1987–1988 (0.11; Rhodes et al. 1991) are the highest reported for this species. Prior electrophoretic data have produced estimates of *H* in American Wigeons at 0.02 for 18 loci (Patton and Avise 1985), and at 0.00 for 10 loci (Numachi et al. 1983). Heterozygosity levels also are high compared to previous estimates for other waterfowl species (0.03; Patton and Avise 1985) and for avian species in general (0.05; Nevo et al. 1984).

Body mass (Haramis et al. 1986), relative condition (Bergan 1990), and carcass reserves (Ankney et al. 1991, Conroy et al. 1989) are thought to be important to overwinter survival and reproduction in many waterfowl species. If genetic variation is related to survival or reproductive success of American Wigeons, it is likely that carcass reserves would be correlated with *H*. This hypothesis is derived by evidence of relationships between genetic variation and secondary productivity or metabolic efficiency in a variety of organisms (Garton 1984, Garton et al. 1984, Mitton and Grant 1984, Allendorf and Leary 1986, Hawkins et al. 1986, Teska et al. 1990).

Waterfowl that winter in the Southern High Plains region are affected by low temperatures, snowfall, high wind speeds, and (to a lesser extent) limited food resources (Baldassarre and Bolen 1984, Whyte and Bolen 1984). Wigeon breeding-habitat conditions immediately preceding our study (1988) were categorized by severe drought. Evidence suggests that body condition of Mallards migrating into the Southern High Plains in 1988 was at a three-year low (Bergan 1990). Mitton and Grant (1984) predicted that relationships between *H* and fitness-correlated characteristics should be more

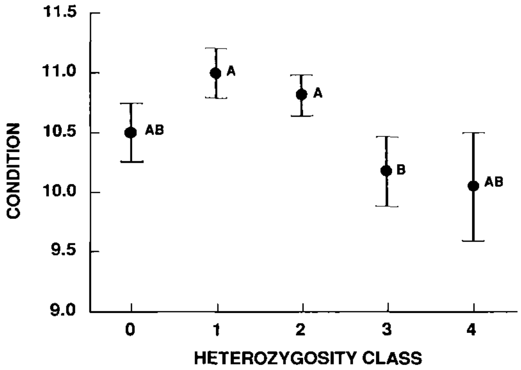

Fig 1. Mean condition values (carcass mass/[body length + wing-chord length]; ±SE) of American Wigeon from late winter for each multilocus heterozygosity class. Significant differences in condition among birds in different multilocus heterozygosity classes indicated by different characters. Wigeons collected on Southern High Plains of Texas during fall and winter of 1988–1989.

TABLE 4. Numbers of American Wigeons collected for each sex (male, female), season, and multilocus heterozygosity class on Southern High Plains of Texas during fall and winter of 1988–1989. Percent of row totals in parentheses.

H	Sex	Autumn	Early winter	Midwinter	Late winter	Early spring
0	Male	9 (16)	11 (20)	16 (29)	11 (20)	8 (15)
	Female	6 (33)	4 (22)	2 (11)	3 (17)	3 (17)
1	Male	11 (9)	24 (20)	27 (23)	25 (21)	31 (26)
	Female	11 (18)	17 (28)	21 (34)	5 (8)	7 (12)
2	Male	30 (23)	17 (21)	27 (21)	31 (24)	24 (19)
	Female	8 (15)	8 (15)	9 (17)	14 (27)	13 (25)
3	Male	26 (32)	17 (21)	16 (20)	7 (9)	15 (18)
	Female	10 (26)	7 (18)	5 (13)	8 (21)	9 (23)
≥4	Male	12 (24)	13 (26)	11 (22)	6 (12)	8 (16)
	Female	7 (31)	5 (22)	4 (17)	4 (17)	3 (13)

distinct during periods of extreme environmental conditions. Evidence supporting this prediction has been presented for organisms such as old-field mice (*Peromyscus polionotus*; Teska et al. 1990), white-tailed deer (*Odocoileus virginianus*; Cothran et al. 1987); and American oysters (*Crassostrea virginica*; Rodhouse and Gaffney 1984).

Relationships between *H* and carcass-component reserves in American Wigeons did not confirm our *a priori* expectations. One explanation is that there is no relationship between *H* and the characteristics measured in these wigeons. Also, it could be that the condition measures used in this research are not directly related to fitness. Although these possibilities exist, numerous studies have demonstrated relationships between *H* and fitness-related characters in other organisms, and the carcass components surveyed in this study are widely thought to be related to survival in many waterfowl species. A third explanation for our results is that the changes in carcass composition through the sampling period are adaptive in origin rather than stress related; however, much of the evidence for such adaptive mass loss comes from research on breeding birds (Croll et al. 1991, Freed 1981). A more parsimonious explanation for the lack of clear relationships in our data may be the mixture of breeding populations in the sample.

American Wigeons that winter on the Southern High Plains come from several breeding grounds. Bellrose (1980:200) stated "The central flyway receives about 3 percent of the Wigeon breeding in Alaska, and an unknown proportion of those nesting in the Northwest Territories, about 12 percent of Alberta's breeding birds, 28 percent of Saskatchewan's, and 22.5 percent of Manitoba's breeding population." Mating systems, philopatry, dispersal, selection, and genetic drift interact to produce the patterns of genetic variation and genetic structure observed in wild populations (Crow and Kimura 1970, Barrowclough 1980, Chesser 1991). Currently, there are no data pertaining to genetic structure or gene flow within or among populations of American Wigeons. However, Rhodes (1991) provided evidence that 12% or more of the total genetic variation in Mallards wintering in the Southern High Plains was partitioned among their original breeding populations. In addition, clinal structural differentiation has been documented for Canada Geese (*Branta canadensis*; Johnsgard 1978) and, possibly, for American Black Ducks (Palmer 1976).

A sampling bias created by the differential distribution of American Wigeons from populations with different genetic characteristics among seasons and regions could explain the lack of strong relationships between genetic and carcass components in these wintering birds. Wigeon populations from geographically disjunct breeding areas would have been subjected to different environmental conditions. These populations may have different evolutionary histories and, potentially, could have different morphological or physiological attributes. This hypothesis is supported by the log-linear analyses involving the distributions of wigeon specimens in *H* classes among seasons and regions on the study area. The number of wigeons in *H* classes differed among seasons and regions. This could be a result of the movement of groups of birds with different genetic characteristics into or out of the study area during the sampling period, or of the differential representation of birds from various regions across the study area among seasons.

These data are among the first reporting on relationships of genetic variation and carcass components in avian species. There is evidence that these types of relationships exist in Mallards (Rhodes 1991). Multilocus genetic variation is negatively correlated to body masses and fat-free body masses of wintering female and juvenile Mallards. Our data, however, do not suggest that strong relationships exist between H and carcass components of wintering wigeons. Differences in the numbers of wigeons in different H classes among regions of the study area suggest that the wintering population is not a homogeneous mixture of birds from genetically similar breeding locations. Based on the results of our analyses, we recommend that future studies of the relationships between H and fitness-related traits in waterfowl should focus on variation within and among breeding populations.

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