

## GENETIC VARIATION IN A WINTER POPULATION OF MALLARD DUCKS

Laurie E. Parker, Eric G. Bolen, and Robert J. Baker

**ABSTRACT.**—We examined the level of heterozygosity in mallard ducks (*Anas platyrhynchos*) to test the hypothesis that species with large panmictic breeding populations will have a relatively high level of genic variation. Based on starch-gel electrophoresis of 20 presumed loci, results indicate a low level of genic variability. Therefore, the predicted relationship of high genic variability in a species with a large effective breeding population size was not found.

A long-standing axiom of population genetics theory is that species with small effective population sizes have low levels of genetic variation when compared to species with large populations. Small, isolated populations display low heterozygosity (Selander and Johnson, 1973). Genetic drift and the founder effect both have been suggested as causes of the reduced variation. Nei et al. (1975) demonstrated that genetic variation theoretically should be reduced in smaller populations and that large populations should exhibit more variation because more neutral mutations may be produced. An examination of a large, nearly panmictic species with high dispersal abilities should lend insight to the relationship between large population size and level of genetic variation contained therein. We accordingly selected the mallard duck (*Anas platyrhynchos*) to test the occurrence of this relationship.

Mallard ducks occur in large numbers throughout their broad range of distribution in the temperate zones of both Nearctic and Palearctic regions (Johnsgard, 1978:218). In North America, a 19-year study of mallard breeding populations indicated that the continental population has ranged from a high of 14.4 million (1958) to a low of 7.1 million birds (1965); the average for the period was nearly 9 million (Pospahala et al., 1974). The species' behavioral patterns also promote panmixia and the approximation of a true Mendelian population. Female ducks of several species, among them mallards, annually return to the nesting grounds, often establishing their nests within the same meadow as in previous years (Sowls, 1955). However, mallard hens select new mates each year so that their pairbonds last for one nesting season only; their drakes may be of far broader geographical origins, thus enhancing an annual mix of genetic material within the breeding population. Hochbaum (1955) has suggested that the females' migrational homing and the selection of new mates each year in mallards and other ducks largely precludes the formation of recognizable races such as occurs in the Canada goose (*Branta canadensis*). Further, the relatively high annual mortality (about 50%, but which varies with age, sex, and regional hunting pressure) of mallards enhances rapid population turnover and the constant introduction and mixing of genetic materials. The mallard population in North America and elsewhere should seemingly support a large number of

TABLE 1.—*Buffer systems, tissues and enzymes used in this study.*

Buffer system	Tissue	Enzymes
LiOH	heart	malic enzyme-1 and -2 (me-1 and -2)
LiOH	heart	tetrazolium oxidase (TO, also called indophenol oxidase, Ipo)
Jrp	heart	mannose phosphate isomerase (Mpi)
Jrp	heart	phosphoglucosomase (Pgm)
Jrp	heart	6-phosphogluconate dehydrogenase (6-Pgd)
T.C.8.O	heart	albumin (Ab)
T.C.8.O	liver	glutamate dehydrogenase (Gdh)
T.C.8.O	liver	glucose-6-phosphate dehydrogenase (G-6-P)
T.C.8.O	liver	glutamate oxalate transaminases -1 and -2 (Got-1 and -2)
T.C.8.O	liver	isocitrate dehydrogenase-1 and -2 (Idh-1 and -2)
Pgi	liver	$\alpha$ -glycerophosphate dehydrogenase ( $\alpha$ -Gpd)
Pgi	liver	leucine aminopeptidase (Lap)
Pgi	liver	lactate dehydrogenase -1 and -2 (Ldh-1 and -2)
Pgi	liver	malate dehydrogenase (Mdh)
Pgi	liver	peptidase (Pep)
Pgi	liver	sorbitol dehydrogenase (Sdh)

neutral mutations with considerable heterozygosity unless directional selection is in effect (cf. Soule, 1976).

**STUDY AREA.**—Mallard ducks of both sexes were collected in Castro County, Texas, in the heartland of a major wintering area. This region of the Texas Panhandle is dotted with shallow depressions known as playa lakes that provide the winter habitat for nearly one-half million mallards in peak years and sustains an average winter population of 280,000 birds of this species (Bolen et al., 1979). Mallards wintering in this region disperse in a broad geographical area of North America, as determined by band recoveries, that includes those states and provinces in the Central Flyway and parts of the Pacific and Mississippi flyways to the north and east.

**METHODS.**—Our results are based on 55 mallards (46 males, 9 females) collected in the fall of 1978. Tissue samples from heart, liver, and breast muscle were frozen in liquid nitrogen in the field for subsequent laboratory analysis using the horizontal starch gel electrophoretic methods of Selander et al. (1971). Heart and muscle samples were combined in the analysis.

Enzymes, tissues, and gel buffer systems used in the study are summarized in Table 1. Stain and gel type recipes are those of Shaw and Prasad (1970), Selander et al. (1971), and Manlove et al. (1976).

A locus was considered polymorphic when the frequency of the most common allele was less than 0.99. Gene frequencies were determined by direct count. Average heterozygosity ( $H$ ) is defined as the average proportion of loci at which individuals were heterozygous; alleles are designated alphabetically in descending order of mobility.

**RESULTS AND DISCUSSION.**—Genetic variation was examined at 20 loci, of which four (20%) were polymorphic. Banding patterns of the polymorphic loci were analogous to those described by Selander et al. (1971), and the frequency of alleles was 93 and 7 for 6-Pgd; 90 and 10 for Mpi; 98 and 2 for Ab where two electromorphs were present; and 90, 8, and 2 for Pep where three electromorphs were found. Additionally, a single variant individual was heterozygous at the Mdh, Sdh, and G-6-P loci. Variation in Ab (albumin) was caused by the presence of one individual homozygous for a slower allele, a phenomenon sufficiently improbable to disrupt the Hardy-Weinberg equilibrium for the Ab locus. Other loci showed no deviations from Hardy-Weinberg equilibrium. Heterozygosity in our sample was 2.7%.

Mallard ducks possess little genetic variation. They show low variability both in individual heterozygosity and in proportion of polymorphic loci. Further evidence of genetic uniformity is the existence of few named subspecies or races. Johnsgard (1967) concluded that four or five subspecies of *Anas platyrhynchos* should be recognized within the North American continental population: the nominate, plus the Mexican duck (*A. p. diazi*); the Florida duck (*A. p. fulvigula*); the mottled duck (*A. p. maculosa*); and possibly the black duck (*A. p. rubripes*). The latter four taxa are characterized by nondimorphic sexual plumage patterns (female-like in both sexes) that are the result of few genetic differences (differences at only two loci between the mallard and black duck can account for the crossbreeding results reported by Johnsgard, 1967). The familiar green-head plumage in males is limited to the nominate race we sampled and to *A. p. conboschas*, an insular form resident in coastal Greenland; the nominate race otherwise breeds in north-temperate Asia, North America, and Europe without evidence of subspeciation.

Hybridizations of mallards are extensive, and include 29 crosses with other taxa of the genus *Anas* (Gray, 1958). As might be expected, three of these crosses are with nondimorphic relatives (e.g., black duck, etc.) often regarded as distinct species rather than as subspecies of mallard (cf. Johnsgard, 1967). The remaining species crosses with *Anas* include seven "good" species commonly found in North America. A surprising number of hybrids involving mallards occurs outside their genus or even their tribe, Anatini (cf. Delacour and Mayr, 1945, for taxonomic organization); these include the genera *Aix*, *Alopochen*, *Anser*, *Aythya*, *Cairina*, *Mergus*, *Netta*, *Somateria*, and *Tadorna* among waterfowl and allegedly with *Numida* and *Gallus* of the order Galliformes. Such extensive hybridization would increase the genetic variability if introgression were occurring. The level of genetic variability in our sample does not suggest extensive introgressive hybridization.

An examination of genetic variation in birds (Nottenbohm and Selander, 1972; Barrowclough and Corbin, 1978; Avise et al., 1980a, b, c) suggests that levels of heterozygosity in this group fall within the range of other vertebrate species (Selander and Kaufman, 1973).

The information presented in this study is not consistent with the hypothesis that there is a direct relationship between population size and genetic variation. Although mallard ducks have a large continental population numbering in the millions and nearly panmictic breeding habits, they show low levels of genetic variation in comparison to other birds. If population size is the only or even the primary determinant of genetic heterozygosity, then one would predict a higher level of heterozygosity in mallards than in the more restricted bird species. The amount of heterozygosity in ducks may be predicted by the environmental grain theory of Selander and Kaufman (1973). If the hypothesis of Selander and Kaufman is correct, then mallards would be expected to experience a "fine-grained" environment and consequently be adapted for an optimal phenotype for that specific environment. Population size seemingly has no effect on genetic variation in mallards.

We thank Rick Martin, Tom Martin, Clint Mallary, and C. David Simpson for assistance in collecting. Laurie Robbins and Mike Arnold critically read the manuscript. This research was supported in part by Organized Research, College of Agricultural Sciences, the Institute of Museum Research, and NSF Grant No. DEB-76-20580.

#### LITERATURE CITED

- AVISE, J. C., J. C. PATTON, AND C. F. AQUADRO. 1980a. Evolutionary genetics of birds I. Relationships among North American thrushes and allies. *The Auk*, 97:135-147.
- . 1980b. Evolutionary genetics of birds II. Conservative protein evolution in North American sparrows and relatives. *Syst. Zool.*, 29:323-334.
- . 1980c. Evolutionary genetics of birds III. Comparative molecular evolution in New World warblers (Parulidae) and rodents (Cricetinae). *Heredity*, 71:303-310.
- BARROWCLOUGH, G. F., AND K. W. CORBIN. 1978. Genetic variation and differentiation in the Parulidae. *The Auk*, 95:691-702.
- BOLEN, E. G., C. D. SIMPSON, AND F. A. STORMER. 1979. Playa lakes: threatened wetlands on the southern Great Plains. Pp. 23-30, *in Proc. Great Plains Agric. Council, USDA For. Serv., Ft. Collins*, 88 pp.
- DELAOUR, J., AND E. MAYR. 1945. The family Anatidae. *Wilson Bull.*, 57:3-55.
- GRAY, A. P. 1958. Bird hybrids; a check-list with bibliography. *Tech. Commun.*, 13, Commonwealth Bur. Animal Breed. and Genet., Commonwealth Agric. Bur., Bucks, England, 390 pp.
- HOCHBAUM, H. A. 1955. Travels and traditions of waterfowl. Univ. Minnesota Press, Minneapolis, 301 pp.
- JOHNSGARD, P. A. 1967. Evolutionary relationships among the North American mallards. *The Auk*, 78:3-43.
- . 1978. Ducks, geese, and swans of the world. Univ. Nebraska Press, Lincoln, 404 pp.
- MANLOVE, M. N., ET AL. 1976. Starch gel electrophoresis for the study of population genetics in white-tailed deer. Pp. 392-403, *In Proc. 19th Ann. Congr. South East Game and Fish Comm. (W. A. Rogers, ed.)*.
- NEI, M., T. MARUYAMA, AND R. CHAKRABORTY. 1975. The bottleneck effect and genetic variability in populations. *Evolution*, 29:1-10.
- NOTTEBOHM, F., AND R. K. SELANDER. 1972. Vocal dialects and gene frequencies in the chingolo sparrow, *Zonotrichia capensis*. *Condor*, 74:137-143.
- POSPAHALA, R. S., D. R. ANDERSON, AND C. J. HENNY. 1974. Population ecology of the mallard II. Breeding habitat conditions, size of the breeding populations, and production indices. *Resource Publ., Bur. Sport Fish. Wildl.*, 115:1-73.
- SELANDER, R. K., AND W. E. JOHNSON. 1973. Genetic variation in vertebrate species. *Ann. Rev. Ecol. Syst.*, 4:75-91.
- SELANDER, R. K., AND D. W. KAUFMAN. 1973. Genetic variability and strategies of adaptation in animals. *Proc. Natl. Acad. Sci.*, 70:1875-1877.
- SELANDER, R. K., ET AL. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). *Univ. Texas Publ.*, 7103:49-90.
- SHAW, C. R., AND R. PRASAD. 1970. Starch gel electrophoresis of enzymes, a compilation of recipes. *Biochem. Genet.*, 4:297-320.
- SOULE, M. 1976. Allozyme variation: its determinants in space and time. Pp. 60-77, *in Molecular evolution (F. J. Ayala, ed.)*. Sinauer Assoc. Inc., Sunderland, Mass.
- SOWLS, L. K. 1955. Prairie ducks, a study of their behavior, ecology and management. Stackpole Co., Harrisburg, 193 pp.

Addresses of authors: L. E. PARKER AND R. J. BAKER, *Dept. of Biological Sciences and The Museum*; E. G. BOLEN, *Dept. of Range and Wildlife Management, Texas Tech Univ., Lubbock, TX 79409*.