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Harold H. Prince
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GENETIC HETEROGENEITY AND DIFFERENTIATION RESULTING FROM SICHUAN PHEASANT (*Phasianus colchicus strauchi*) INTRODUCTIONS IN SOUTHERN MICHIGAN

By

Catherine Simpson Flegel

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ABSTRACT

GENETIC HETEROGENEITY AND DIFFERENTIATION
RESULTING FROM SICHUAN PHEASANT (*Phasianus cholchus strauchi*)
INTRODUCTIONS IN SOUTHERN MICHIGAN
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Levels of genetic heterogeneity and differentiation were estimated among four populations of common pheasants (*Phasianus cholchus*) in southern Michigan collected from 1991-1993 using starch gel electrophoresis. The pure Sichuan (*P. c. strauchi*) (n = 37) gene pool was evaluated by sampling the captive breeding stock housed at the Michigan Department of Natural Resources, Mason Wildlife Facility. Free-ranging ring-necked (*P.c. torquatus*) (n = 48), and populations that received Sichuan (Sichuan Release, n = 60) or a mixture of Sichaun x ring-necked hybrids (Mixed Release, n = 45) constituted the remaining three populations. Estimates of observed ($\bar{H}_{obs}$) and expected ($\bar{H}_{exp}$) heterozygosity and inbreeding coefficient, F_{IS}, were calculated. Nei's (1978) unbiased (D_N), Rogers (1972) (D_R), Rogers (1972) as modified by Wright (1978) (D_W) and Cavalli-Sforza and Edwards (1967) chord (D_C) distances were calculated. Unweighted pair-group method with arithmetic averaging branching diagrams were constructed using all distance measures, and a branching diagram using D_W was generated using the distance Wagner procedure. Allelic and genotypic data were compared to morphological (neck ring) data.

Thirty enzymes were examined for polymorphism using liver tissue. No unique alleles were detected in the ring-necked (n = 4) or Sichuan (n = 8) individuals used in the initial screening process. $\bar{H}_{obs}$ ranged from 0.019 in the Sichuan Release population to

0.029 in the Captive Sichuan population. $\bar{H}_{exp}$ values were higher and ranged from 0.035 to 0.042 in the Sichuan Release and Captive Sichuan populations, respectively. The deficiency of heterozygotes was also reflected in F_{IS} (-0.114). The majority of loci in the free-ranging populations were not in Hardy-Weinberg equilibrium, while all loci in the Captive Sichuans were in equilibrium. The low proportion of heterozygotes may have resulted from assortative mating, small population size, and/or biased sampling. Neighborhood size was estimated at 3234 pheasants. Given current pheasant density estimates, an area equivalent to 2 townships should have been sampled compared to the 4 that were, suggesting more than one breeding unit was sampled. The deficiency in heterozygotes could have resulted from a Wahlund effect.

Gene flow from the captive Sichuan into the release populations appeared to be substantial as evidenced by the genetic identity measures. Sichuan and Mixed Release populations were intermediate to the Captive Sichuan and ring-necked populations. Diagrams incorporating the morphological data showed a different pattern. F_{ST} averaged 0.298 suggesting that 70% of the total genetic variation was within populations, while 30% was distributed among populations.

To my late husband, Thomas Dale Flegel

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INTRODUCTION

In 1925, Michigan held its first ring-necked pheasant (*Phasianus colchicus*) hunting season (MacMullan 1957) and this species soon became the most popular upland game bird in the state (McCabe et al. 1956). The success of common pheasants in Michigan is owed in part to the state-sponsored introduction of ring-necked pheasants that began in 1918 (McCabe et al. 1956, MacMullan 1957). State and Midwest pheasant populations increased to record numbers during the mid-1940s. Populations have since declined, sometimes rapidly, over the past four decades.

Individual factors believed to be associated with declines in pheasant populations include changes in agricultural land use patterns, predation, stochastic climatic events, changes in agricultural chemical applications, and loss of genetic diversity from state sponsored and private propagation and release programs. As farmers shifted from small grains and forage crops to row crop production, optimal pheasant nesting and brood cover declined (Leedy and Dustman 1947, Warner 1979, Warner et al. 1984). Winter cover, as fence rows and small herbaceous wetlands, declined when the agricultural community began practicing clean farming, which promotes use of all available land, and fall plowing (Labisky 1976, Warner and David 1982). Loss of adequate cover led to increased

vulnerability of pheasants to predators (Dumke and Pils 1973, Petersen et al. 1988) and mortality due to exposure and/or starvation during harsh winters (McClure 1948, Kopischke and Chesness 1967). The negative relationship of biocides on survival and reproduction is well documented (Adams and Prince 1972, Stromborg 1977, 1979, Bennett and Prince 1981). Unfortunately, awareness of the individual factors that negatively impact pheasant populations has not enabled state agencies to restore pheasants populations to the levels of the 1940's.

Taxonomy of Pheasants and History of Early Introductions

Pheasants belong in the Tribe Phasianini. While only one species, the ring-necked pheasant, *Phasianus colchicus*, is currently recognized in North America by the American Ornithologists' Union (1982), the genus as a whole is very diverse from a world wide perspective. Delacour (1977) recognized 17 genera and 124 races of pheasants distributed across Asia that belong to the Subfamily Phasianinae. True pheasants of the genus *Phasianus* consist of 2 species; *P. colchicus*, or the common pheasant and *P. versicolor*, the green pheasant (Delacour 1977, Johnsgard 1986). Thirty races of common pheasants (*P. colchicus*) are geographically distributed across Asia into 4 groups; the black-necked (5 races), white-winged (7 races), olive-rumped (1 race), and the grey-rumped (17 races) group (Delacour 1977, Johnsgard 1986) (Table 1, Fig. 1). These 30 races replace one another geographically and have been termed a "superspecies" because of their ability to readily breed and produce fertile hybrids (Delacour 1977).

Introduced populations, representing combinations of several races, exist in Europe from the British Isles and southern Norway, through Sweden, Germany, and Greece, south to Bulgaria (Johnsgard 1986) (Fig. 1). A pure black-necked type from

Table 1. Systematic list of common pheasants *Phasianus colchicus* (from Delacour 1977 and Johnsgard 1986).

Group	Scientific Name	Common Name
Black-necked pheasants	*P. c. colchicus* Linne	Southern Caucasian pheasant
	P. c. septentrionalis Lorenz	Northern Caucasian pheasant
	P. c. talischensis Lorenz	Talisch Caucasian pheasant
	P. c. persicus Severtzov	Persian pheasant
	P. c. principalis Sclater	Prince of Wales' pheasant
White-winged pheasants	*P. c. zarudnyi* Buturlin	Zarudny's pheasant
	P. c. bianchii Buturlin	Bianchi's pheasant
	P. c. chrysomelas Severtzov	Khivan pheasant
	P. c. zerafschanicus Tarnovski	Zerafshan pheasant
	P. c. shawi Elliot	Yarkand pheasant
	P. c. turcestanicus Lorenz	Syr Daria pheasant
	P. c. mongolicus Brandt	Kirghiz pheasant
Olive-rumped pheasant	*P. c. tarimensis* Pleske	Tarim pheasant
Grey-rumped pheasants	*P. c. hagenbecki* Rothschild	Kobdo ring-necked pheasant
	P. c. pallasi Rothschild	Manchurian ring-necked
	P. c. karpowi Buturlin	Korean ring-necked pheasant
	P. c. kiangsuensis Buturlin	Shansi pheasant
	P. c. alaschanicus Alpheraky & Bianchi	Alashan pheasant
	P. c. edzinensis Suchkin	Gobi ring-necked pheasant
	P. c. satscheuensis Pleske	Satchu ring-necked pheasant
	P. c. vlangalii Przevalski	Zaidan pheasant
	P. c. strauchi Przevalski	Strauch's pheasant
	P. c. sohokhotensis Buturlin	Sohokhoto pheasant
	P. c. suehschanenis Bianchi	Sungpan pheasant
	P. c. elegans Elliot	Stone's pheasant
	P. c. rothschildi La Touche	Rothschild's pheasant
	P. c. decollatus Swinhoe	Kweichow pheasant
	P. c. takatsukasae Delacour	Tonkin ring-necked pheasant
	P. c. torquatus Gmelin	Chinese ring-necked pheasant
	P. c. formosanus Elliot	Taiwan ring-necked pheasant

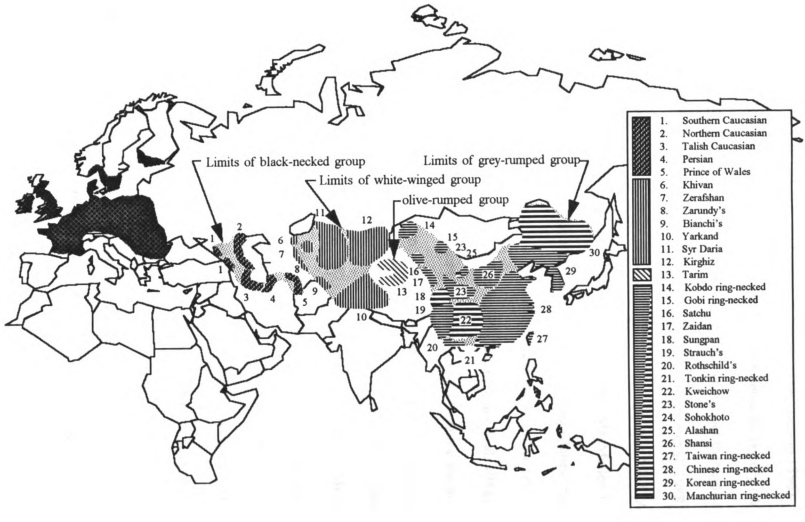

Figure 1. Distribution of *Phasianus* in Asia. The introduced range in Europe (cross-hatched) is of birds of varied origins (from Johnsgard 1986).

Persia dominated in England until ring-necked pheasants from the grey-rumped group were imported from the Orient in the eighteenth century (MacPherson 1896). A diverse mix of at least 3 to 4 races existed in Europe by the late nineteenth century (Wayre 1969, Bohl and Bump 1970) and it was from this heterogenous gene-pool that introductions were made into the U.S. in the late 1980's and early 1900's (Prince et al. 1988).

Michigan began a successful pheasant introduction program in 1918 (Allen 1956). By 1925, populations of pheasants had reached huntable levels (MacMullen 1957). Michigan game farm ring-necks exhibit a mixed heritage including Chinese ring-necked (*P. c. torquatis*), Korean ring-necked (*P. c. karpowi*), English black-necked (*P. c. colchicus*) and Mongolian or Kirghiz ring-necked (*P. c. mongolicus*) (Prince et al. 1988). Males differ in plumage (Table 2) while females have a brown spotted mantle and an under body which is not mottled (Johnsgard 1986). Population sizes gradually increased with fluctuations until 1935, and then dramatically declined in the 1940's with a peak harvest of 1,404,076 males in 1944 (MacMullen 1957). Spring estimates of hens in Michigan fell from 713,600 in 1961 to 145,500 in 1986 (Dahlgren 1988). This decline was similar to those seen throughout the ring-neck's Midwest range (Dahlgren 1988).

In the 1960s, interest in introductions of exotic game birds renewed (Prince et al. 1988). Allen (1956) suggested that releases in America of races of pheasants living in remote parts of Asia, and not yet released in America, might be useful. This suggestion lead to the formation of "The Foreign Game Introduction Program" (FGIP) of the U.S. Fish and Wildlife Service in the mid-1950s (Prince et al. 1988). The program was designed to limit unwise introductions, while promoting trial introductions of previously unavailable pheasants into vacant habitats. Five races were subsequently imported into the

Table 2. Neck ring characteristics of some common pheasants introduced into North America.

Group	Neck Ring		Scientific Name	Common Name
	Present	Width at Front		
Black- necked	No	--	*P. c. colchicus*	Southern Caucasian or European Blackneck pheasant
White- winged	Yes	wide	*P. c. mongolicus*	Kirghiz or Mongolian pheasant
Grey- Rumped	Yes	wide	*P. c. karpowi*	Korean ring-necked pheasant
	Yes	narrow	*P. c. torquatus*	Chinese ring-necked pheasant
	No	--	*P. c. strauchi*	Strauchi's or Sichuan pheasant

U.S. including 2 races of black-necks (*P. c. talischensis*, Talish Caucasian and *P. c. persicus*, the Persian pheasant), 1 white-winged (*P. c. bianchi*, Bianchi's pheasant) and 1 grey-rumped (*P. c. karpowi*, Korean ring-necked pheasant). In addition, the Northern green pheasant, *P. versicolor robustipes*, was imported from Japan (Prince et al. 1988).

Work by Warner et al. (1988) identified regional differences in genotype among wild pheasants established from releases in Illinois. These differences could be attributed to differences between founding populations and/or selection following release. Prince et al. (1988) hypothesized that the establishment of pheasant populations, or the revitalization of declining pheasant populations is, to a large part, a function of genotype. The release of newly imported races, along with selective breeding of genotypes, was

proposed to be critical to future pheasant management programs.

Background of Michigan's Sichuan Pheasant Release Program

The Michigan Department of Natural Resources (MDNR) embarked on a new program in 1983 to bolster pheasant populations in Michigan using the Strauch's, pheasant (*P. c. strauchi*), a race of common pheasant within the grey-rumped group found in the Zhenja District of the northeastern region of Sichuan Province, People's Republic of China (Squibb 1985, Prince et al. 1988). This race has been given the honorary appellation of Sichuan pheasant in recognition of the generosity of The People of Sichuan Province for providing birds (Prince et al. 1988).

In 1983, the improved political climate between the United States and the People's Republic of China offered the MDNR an opportunity to acquire a subspecies of pheasant from Guangyuan County not yet introduced on the North American continent. Climatic differences between Guangyuan County, based on 3 years of weather records for Chengdu, Sichuan Province (adjusted for the 970 m elevation difference) and Ingham County, Michigan, are minor. Late winter and early spring mean temperatures in Lansing, Michigan (Sommers 1977) are slightly cooler by 3.7^0 and 2.9^0 C for January and April, respectively, compared with Guangyuan County. Annual rainfall for both areas averages 81.2 - 86.4 cm. However, 80% of the annual rainfall in Guangyuan occurs from July to September (Chen 1970), while annual rainfall in Michigan is more evenly distributed.

Chinese officials offered Michigan 200 wild pheasant chicks. Approximately 300 eggs of Sichuan pheasants were collected in the Zhenja District of Sichuan Province in the spring of 1984. Eggs were hatched and chicks were reared by the Sichuan Forestry Department. Rearing problems were encountered and only 30 chicks survived to be

shipped to Hawaii where they were quarantined for at least one month. In February of 1985, Michigan finally received 24 Sichuan pheasants, 9 males and 15 hens.

In the spring of 1985, an American delegation traveled to Zhenja District, in the northeastern part of Sichuan Province, People's Republic of China, on a mission to collect Sichuan pheasant eggs. Approximately 2300 eggs were obtained from more than 500 nests. Eggs were subsequently shipped to Michigan from which 550 chicks were pedigree hatched by family unit at the Rose Lake Wildlife Research Station. The chicks were transferred to the Mason Wildlife Facility following the quarantine period. By February 1986, a second group of P_1 Sichuans (n = 420) were available for captive breeding.

Michigan biologists returned to Zhenja District in the spring of 1988 for a second collection of eggs. More than 1,300 eggs were collected and shipped to Michigan. These efforts resulted in a third group of P_1 pure Sichuans (n = 363) available for captive breeding in February of 1989.

The Sichuan pheasant propagation program was designed to maintain genetic heterogeneity in a breeding and rearing environment that would facilitate release. The captive breeding program focused on holding breeders for as many seasons as possible to reduce inbreeding, selection, and genetic drift within the captive population (Prince et al. 1988). The propagation program was adaptive in the sense that space and habitat modifications in breeding and rearing areas were made as the program continued. The captive Sichuan population for this study included F_1 progeny of Sichuan breeders originally obtained by the MDNR from China.

In its native range, the Sichuan pheasant inhabits brushy, agricultural and mountainous pine (*Pinus* spp.) and oak (*Quercus* spp.) forests, a habitat type different

from perceived bush, grass and agricultural habitat preferences of the introduced races, primarily the Chinese ring-necked pheasant (*P. c. torquatus*), that were released in North America from the late 1800's until the present. Sichuan pheasants had not been subjected to any captive propagation programs and for this reason were thought to represent a unique gene-pool.

Genetics of Successful Introductions and Objectives of this Study

A key to the success of the Sichuan introduction program will be the maintenance of genetic variability, to afford the populations with the maximal chance of adaptation. Genetic variability in populations can decay through selection, inbreeding, or random drift especially if the population size becomes small. A reduction in genetic heterozygosity in Michigan's existing ring-necked compared to the Sichuan pheasant would be expected if local pheasant populations in Michigan have undergone recent population bottlenecks or are suffering from inbreeding depression resulting from generations of captive breeding.

While propagation and release programs that mix stocks can result in the dilution of co-adapted gene complexes, the infusion of new genetic material into a breeding population may prove advantageous in offsetting the loss of genetic variability by increasing heterozygosity. Increased levels of heterozygosity lead theoretically to increased fitness, decreased frequency of deleterious alleles, and reduced inbreeding depression.

The introduction of yet another race of pheasant in Michigan offered an opportunity to measure the genetic differences in common pheasants, and to generate hypotheses associated with the introduction of a new race. Direct sampling of the original races from Asia, although desirable, was beyond the scope of this project. However, it

was possible to compare the genetic composition of a race (ring-necked) that has been subjected to the continuous anthropomorphic influences of captive propagation with one that has not (Sichuan). Michigan's current free-ranging ring-necks were used to represent populations of mixed racial heritage established via releases from traditional game farms. P_1 and F_1 breeders from Michigan's captive Sichuan pheasant program were used to represent populations that were new to the captive breeding environment and considered to be a pure race.

Introductions of Sichuan pheasants into free-ranging populations led to the following predictions. First, a reduction in genetic heterozygosity in Michigan's existing local ring-necked pheasant populations compared to the captive Sichuan breeding stock would be expected if local ring-necks had undergone recent population bottlenecks or were suffering from inbreeding depression as a consequence of generations of captive breeding. Secondly, the infusion of new genetic material into a free-ranging breeding population may prove advantageous in offsetting the loss of genetic variability by increasing heterozygosity. Increased levels of heterozygosity lead, theoretically, to increased fitness. Finally, since these two races freely interbreed in captivity and produce fertile hybrids, levels of genetic heterozygosity and the distribution of genetic variance in free-ranging populations should vary since the infusion of the Sichuan genetic component was controlled by the number and genetic heritage of birds released from the captive breeding program. An assessment of phenological traits in differentiating subspecies or populations was also possible by comparing neck-ring characteristics of male pheasants with their biochemical profile.

ISOZYME VARIABILITY IN HARVESTED RING-NECKED AND SICHUAN PHEASANTS

INTRODUCTION

Starch gel electrophoresis provides a tool to assess the biochemical genetic variability of captive and wild pheasants. The use of plumage or other traits to describe genetic variation has been insufficient (Trautman 1982) and often the phenotypic expression of meristic and morphometric traits are too variable to be reliable (Ihssen et al. 1981). Visible genetic variation affecting phenotypic traits are often influenced by many genes, as well as by the effects of the environment, so phenotypic differences for such traits can rarely be traced to the effects of particular genes (Hartel 1987). Since the advent of starch gel electrophoresis in 1959, the technique of electrophoresis has been used to provide useful information on variability patterns in a wide range of biological situations (Richardson et al. 1986).

The banding patterns from separation of proteins after exposing the medium to histochemical specific stains, can be related to frequencies of various alleles at single loci, and each individual can be assigned a genotype. Estimation of heterozygosity, genetic distance, and the calculation of the among and within components of genetic variation is possible.

Early electrophoretic analyses indicated differences in pheasant genotypes in North America. Brandt et al. (1952), Sandness (1954), and Baker et al. (1966) used proteins from eggs and sera to describe genetic differences between pheasants and their hybrids. Blood group factors indicated regional differences in pheasants from Iowa (Vohs 1966). An east-west gradient in the frequency of fast-binding forms of blood protein was found in pheasants from Illinois, Iowa, and Kansas (Baker et al. 1966). Warner et al. (1988) identified a north-south cline for wild pheasants in Illinois using isozyme methods.

The genetic heritage of North America's ring-necked pheasant (*P. colchicus*) is, at best, a blend of races dominated by *P. c. torquatus* (Chinese ring-necked pheasant) that originated in Asia. The use of electrophoretic procedures have identified differences in wild pheasant populations resulting from range expansions from releases in the 1930's through the early 1950's (Warner et al. 1988). There is no clear explanation of how these differences emerged and several factors must be considered including initial stock differences, founder effects, and selection in response to environmental gradients. It is clear, however, that starch electrophoresis is a useful tool for describing patterns of variability in wild pheasant populations, and where race specific markers exist, it can be used to measure the integration of a new race of pheasant into existing populations. This methodology was used in this study to assess the genetic structure of 4 populations of common pheasants in Michigan.

ELECTROPHORETIC METHODOLOGY

An initial electrophoretic screening was performed using Sichuan and ring-necked breeders housed at MDNR's Mason Wildlife Facility. All ring-necks were wild trapped birds obtained from various locations throughout Michigan in the winter of 1989 in an

attempt by the MDNR to improve their captive ring-necked stock. Tissue samples were obtained from birds within 4 hours of death. Leg band numbers were recorded for comparison of pedigrees.

A detailed description of starch electrophoretic techniques, including grinding buffers and gel preparation are presented in Appendix A. Individuals were initially screened for variation at 30 biochemical loci using 15 electrode buffer systems. Staining was also done for enzymes found to be polymorphic in other galliformes (Baker and Manwell 1975, Gutierrez et al. 1983, Gyllensten 1985, Zink et al. 1987, Warner et al. 1988, Scribner et al. 1989, and Randi et al. 1991, 1992). The objective of this process was to refine laboratory procedures and find enzymes that were polymorphic in which clear banding patterns could be replicated.

The liver was removed from all birds and stored at -70^0 C at MSU for the duration of this study. Care was taken to insure an airtight condition to prevent dehydration. Four milligrams of liver tissue was homogenized in a grinding buffer on ice using a pestle and mortar the day before an electrophoretic run. Contamination of the sample was reduced by avoiding connective and adipose tissue. Paper wicks were saturated with the resulting supernatant, placed in individual wells in ELISA trays, double wrapped in plastic and frozen at -70^{0}C for use the next day.

Starch gels were prepared 12 hours before each electrophoretic run. Once the liquid starch had solidified and cooled, the gels were covered with plastic wrap to prevent desiccation. Gels were kept at room temperature until 1 hour before the start of the run, when they were cooled to 4^{0}C.

Gels were continuously cooled over an ice bath for the duration of each run.

Wicks were removed 20 minutes after the beginning of the run that lasted 6 ½ hours. Completed gels were sliced horizontally, placed in enzyme stains, and incubated in the dark. Acetate was used to halt the staining process. Gels were fixed using 50% ethanol, placed in air tight plastic storage bags, labeled, and stored at 4^0C.

Gels were scored immediately after staining. When more than one putative locus was observed for a particular enzyme, they were numbered sequentially, beginning with the most anodal. Alleles at variable loci were coded by letters beginning with "a" for the most anodal. All genotypes were scored for all the loci.

ELECTROPHORETIC RESULTS AND DISCUSSION

Although thirty enzymes were examined (Table 3), only 5 loci, representing 4 enzymes; alkaline phosphatase (AP), acid phosphatase (ACP), aconitase (ACON 1 and 2), and isocitrate dehydrogenase (IDH 1); were consistently scoreable and polymorphic. Staining for enzyme activity followed methods outlined by Richardson et al. (1986). Esterase appeared to be polymorphic and sub-banding was excessive which confounded scoring. While the enzymes found to be polymorphic in other galliformes were systematically stained in all our free-ranging pheasant collections, none proved to be polymorphic except AP, ACP, ACON and IDH.

ACON, IDH, AP, and ACP were found to be polymorphic in many other galliformes (Baker and Manwell 1975, Gutierrez et al. 1983, Gyllensten 1985, Zink et al. 1987, Scribner et al. 1989, Randi et al. 1992,) but not in all (Warner et al. 1988, Randi et al. 1991). Differences between studies may be attributable, in part, to the composition of tissues used and laboratory conditions. Since an enzyme's expression varies between tissues, the ability to detect polymorphisms may have been limited by using only liver

tissue. Barrowclough and Corbin (1978) found ACP and IDH were most commonly found in liver tissue. Scribner et al. (1989) found AP to be polymorphic in ring-necked pheasants using tissues from the liver, heart and kidney. ACON was polymorphic in a homogenous mix of heart, liver, kidney, and muscle in California quail (*Callipepla californica*) (Zink et al. 1987).

No unique alleles were detected in the ring-necked or Sichuan individuals used in the initial screening process (Table 4). This is surprising as different, but closely related species of animals typically show fixed differences, or almost fixed differences, for at least some of their electrophoretic loci (Ayala 1975, Richardson et al. 1986). However, bird species are commonly indistinguishable at allozyme loci (Avise et al. 1982). Why birds are different from other vertebrates is unknown, but it is generally accepted that birds at all taxonomic levels exhibit less genetic divergence than do many of their counterparts in other vertebrate classes (Avise and Aquardro 1982, Barrowlclough et al. 1985, Prager et al. 1974).

It is likely that markers between ring-necked and Sichuan pheasants can be found since they are recognizable at the subspecies level. However, it may require a different type of molecular analysis to identify species or subspecies specific alleles. Many researchers found diagnostic mitochondrial DNA (mtDNA) markers when earlier allozyme surveys of congeneric waterfowl, sparrows, and warblers had failed (Kessler and Avise 1984, 1985). Mack et al. (1986) reported a large number of mtDNA restriction site differences between 2 titmouse species (*Parus atricapillus* and *P. carolinensis*) that were indistinguishable in a survey of 35 allozyme loci (Braun and Robbins 1986).

Table 3. Enzymes evaluated for genetic analysis of common pheasants in southern Michigan.

Code	E.C. No.[a]	Enzyme	Electrode Buffer Systems Attempted[b]	Resolution[c]	Activity[d]
ACON	4.2.1.3	aconitase / aconitate hydratase	**A B C** D G I M O	Good	P
ALD / FBA	4.1.2.13	aldolase / fructose-bisphosphate aldolase	**A C** D N	Poor	?
ADA	3.5.4.4	adenosine deaminase	**A C** G M O	Poor	?
ACP	3.1.3.2	acid phosphatase	**A B C** M N O	Good	P
ADH	1.1.1.1	alcohol dehydrogenase	**A B C** E F G H L M N	Fair	M
AP	3.1.3.1	alkaline phosphatase	**A B C** F J M N	Good	P
AAT / GOT	2.6.1.1	aspartate aminotransferase / glutamate	**B C F** K	Fair	?
CK	2.7.3.2	creatine kinase	**C M** N	Fair	?
EST	3.1.1.-	esterase	**B** F G J M N O	Fair	P
FDP / FBP	3.1.3.11	fructose 1,6 biphosphate / fructose-bisphosphatase	**A** D G N O	Fair	?
FUM	4.2.1.2	fumarate hydratase / fumarase	**A** E G N O	Poor	?
GDH	1.4.1.2	glutamate dehydrogenase	**B C** E M N	Poor	?
"GPD	1.1.1.8	" glycerol-3-phosphate dehydrogenase	**C** E G M N	Fair	M
G3PDH	1.2.1.12	glyceraldehyde-3-phosphate dehydrogenase	**A C** M N	Fair	M
G6PDH	1.1.1.49	glucose-6-phosphate dehydrogenase	**A B C** E F G N	Fair	M
HEX	2.7.1.1	hexokinase	**C** G I N	Fair	?
IDH	1.1.1.42	isocitrate dehydrogenase	**A B C** H M O	Good	P
LDH	1.1.1.27	lactate dehydrogenase	**C** E F G H I M N O	Good	M
MDH	1.1.1.37	malate dehydrogenase	**A B C** E F I M N O	Good	M
MPI	5.3.1.8	mannose phosphate isomerase	**B** E O	Good	M
ME	1.1.1.40	malic enzyme	**A C** G M N	Good	M
PGI / GPI	5.3.1.9	phosphoglucoisomerase / glucose-6-phosphate	**A B C** F G O	Good	M
PGM	2.7.5.1	phosphoglucomutase	**A B C** F G M N	Good	M
6PGD	1.1.1.44	6-phosphogluconate dehydrogenase	**A** E G N	Good	M
PEP	3.4.-.-	peptidase	**A B C** M O	Good	M
PGK	2.7.2.3	phosphoglycerate kinase	**A** O	Poor	?
SDH /SORH	1.1.1.14	sorbitol dehydrogenase / L-iditol dehydrogenase	**A B** E H M N	Poor	?
SOD	1.15.1.1	super oxide dismutase	**A B** G M N O	Fair	M
TPI	5.3.1.1	triose phosphate isomerase	**B C** E F G I N O	Good	M
XDH	1.1.1.204	xanthine dehydrogenase	**B** E F M N	Good	M

[a] Enzyme Commission Number [b] Enzyme most resolvable in bolded buffer; A) Morpholine-citrate pH 6.1 (Clayton and Tretiak 1972); B) Lithium-borate pH 8.3 (Scandolis 1969); C) Tris-citrate pH 7.0 (Miezel and Markert 1967); D) Tris-citrate pH 8.0 (Shaw and Prasad 1970); E) Tris-versene-borate pH 8.0 (Selander et al. 1971); F) Sodium borate pH 8.0 (Poulik 1957); G) Phosphate pH 7.0 (Richardson et al. 1986); H) Phosphate-citrate pH 8.0 (Shaw and Prasad 1970); I) Tris-maleate-EDTA-$MgCl_2$ pH 7.8 (Richardson et al. 1986); J) Sodium-borate pH 8.65 (Ayala et al. 1972); K) Tris-borate pH 7.5 (Shaw and Prasad 1970); L) 0.5 M Phosphate pH 7.0 (Shaw and Prasad 1970); M) Tris-maleate pH 7.8 (Richardson et al. 1986); N) Tris-EDTA-borate-$MgCl_2$ pH 7.8 (Shaw and Prasad 1070); O) Citrate-phosphate pH 6.4 (Richardson et al. 1986). [c] good = consistently scorable, Fair = not consistently scorable, Poor = generally smeared; [d] P = polymorphic, M = monomorphic, ? = unknown

Table 4. Allele and genotypic frequencies, at polymorphic loci, of Sichuan and ring-necked pheasants used in the evaluation of enzymes for genetic analysis of common pheasants in Michigan.

Allele Frequencies				Genotypic Frequencies		
Locus/Allele		Sichuan	Wild-trapped Ring-neck	Genotype	Sichuan	Wild trapped Ring-neck
ACP						
	p	0.875	0.750	aa	0.875	0.750
	q	0.125	0.250	ab	0.0	0.0
	n	8	4	bb	0.125	0.250
AP						
	p	0.938	0.750	aa	0.875	0.750
	q	0.063	0.250	ab	0.125	0.0
	n	8	4	bb	0.0	0.250
IDH-1						
	p	0.813	0.750	aa	0.750	0.750
	q	0.188	0.250	ab	0.125	0.0
	n	8	4	bb	0.125	0.250
ACON-1						
	p	0.938	1.0	aa	0.875	1.0
	q	0.063	0.0	ab	0.125	0
	n	8	3	bb	0.0	0
ACON-2						
	p	0.750	1.0	aa	0.625	1.0
	q	0.250	0.0	ab	0.250	0
	n	8	3	bb	0.125	0

ISOZYME VARIABILITY IN PURE AND MIXED PHEASANT POPULATIONS IN MICHIGAN

INTRODUCTION

Releases of Sichuan pheasants into southern Michigan provided an opportunity to evaluate the impact of an introduction on existing ring-necked populations and to measure the genetic differences in common pheasants. Refinement of electrophoretic methods provided the tool to investigate levels of genetic heterogeneity and the distribution of genetic variance within and between populations.

METHODS

Stocks

Two populations were sampled to represent "pure" *P. c. strauchi* (Sichuan) and *P. cholchus* (North American ring-necked pheasant): 1) breeders from Michigan's captive Sichuan propagation program, and 2) samples obtained from hunter harvest of free-ranging, local common pheasants. Two additional free-ranging populations were sampled including one that received a mixture of Sichuan, ring-neck, and hybrid releases, and another which other received only pure Sichuan releases.

Collection of Pheasants for Electrophoresis:

Pure Sichuans: Livers of both male and female, adult pure P_1 and F_1 Sichuan

breeders, from the MDNR's Mason Wildlife Facility were collected during 1990-92. This sample included the birds used in the initial electrophoretic screening process plus birds that died when a mink(s), (*Mustela vison*), gained access into several outside flight pens and killed dozens of 2+ year old breeders during the winter of 1992. Carcasses were partially thawed to allow for the removal of the liver at a later date.

Michigan's Local Ring-necked Pheasants: Samples from Montcalm and Hillsdale counties were used to assess the genetic composition of free-ranging wild ring-necked pheasants in Michigan (Fig. 2). The free-ranging wild ring-neck population included local pheasants in areas thought to have strong remnant ring-neck numbers and habitats not suitable for Sichuan releases.

Samples of free-ranging male pheasants from Montcalm and Hillsdale counties were collected with the assistance of local Pheasant Forever Chapters. Local hunters were supplied with a collection bag before the regular season. The liver was removed within 4 hours of death. Width of the neck ring at its widest point was marked along the edge of each collection bag and measured to the nearest mm at a later date. Hunters were asked to estimate the percent closure of the neck ring in ¼ intervals and indicate the location of each kill. Materials from each individual bird were placed in a corresponding collection bag and stored in a home freezer until the end of the season. All samples were then stored at -70^{0}C at MSU for the duration of this study

Sichuan Release Population: Samples from Livingston and surrounding counties were used to measure the influence of Sichuan releases on local ring-necked populations (hereafter referred to as the Sichuan Release Population) (Fig. 2). All Sichuan releases were F_1 progeny of breeders obtained from China in 1985 and 1988 as eggs. Release

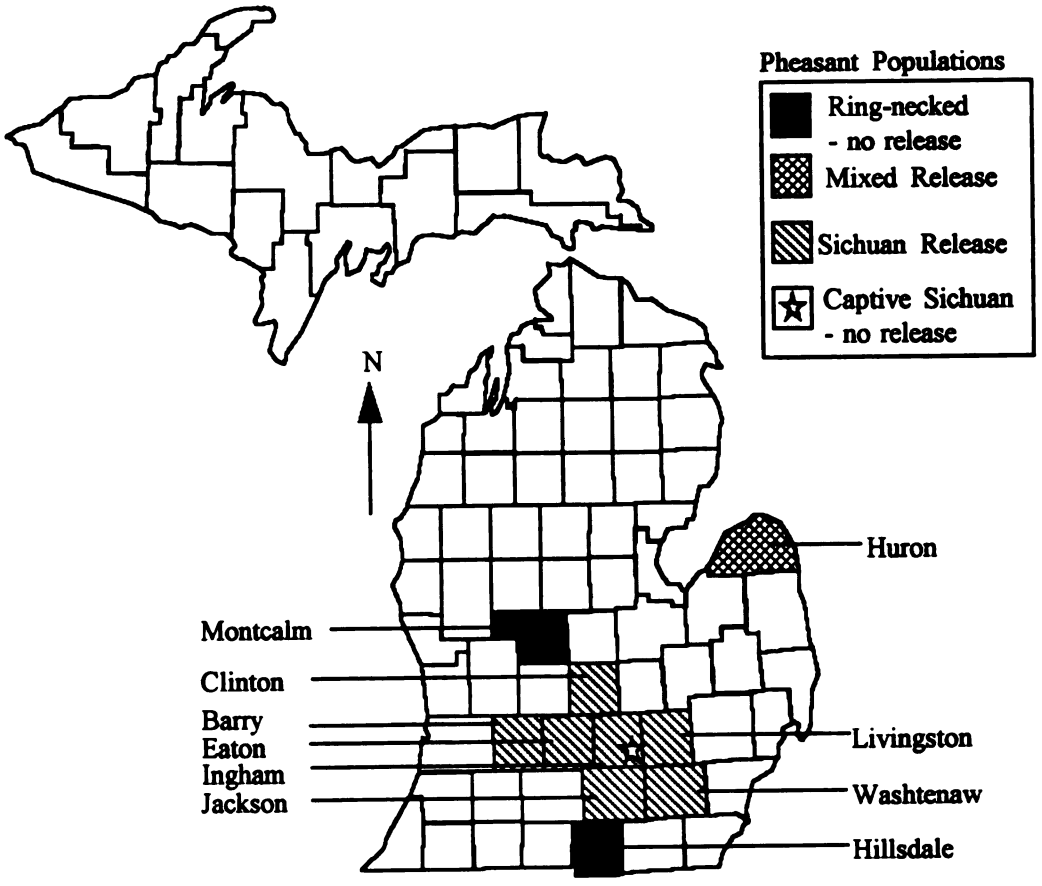

Figure 2. Counties sampled to evaluate free-ranging pheasant populations. Three free-ranging populations, the local ring-necked, the Mixed Release, and the Sichuan Release were sampled in 1991-1993. Pure Sichuan pheasants were assessed by sampling the MDNR's captive breeding population at the Mason Wildlife Facility (denoted by star).

efforts by the MDNR focused on establishing pheasants with Sichuan heritage in habitats in Michigan that were void, or nearly void, of wild pheasants and to maximize founding populations. Potential release sites were evaluated based on the structure of vegetation similar to that in Sichuan Province. Groups of 50-60 pheasants were released and hunting was restricted to minimize mortality and facilitate dispersal (Prince et al. 1988).

From 1986 to 1993, approximately 20,517 pure Sichuan pheasants were released in Livingston and surrounding counties (Fig. 3). Livingston and Jackson received similar numbers of releases (30% and 39% of all releases, respectively). Since the objective of this study was to examine the introgression of the Sichuan genetic material into local common pheasant populations, Livingston County remained the "core" of the Sichuan release population for all releases occurred during 1986-1990 (n=6251). Males harvested during 1991-1993 would reflect the introgression of Sichuan genes into the population.

Samples of free-ranging males from Livingston and surrounding counties were collected with the aid of MDNR personnel. Collection materials were distributed to biologists before the regular season. On opening day, individual hunters were actively sought in the field by MDNR personnel. If successful, hunters were asked to donate the liver from their harvested bird(s). Ring neck width and closure were recorded by MDNR personnel. All materials were placed in a frozen state (-70^{0}C) within 4 hours of death.

Mixed Release Population: Samples from Huron county were used to measure the effect of releases with varied racial heritage on the local remnant ring-necked population (hereafter referred to as the Mixed Release Population) (Fig.2). An effort to improve the captive breeding program was initiated in 1989 by the inclusion of winter trapped "wild" ring-necked birds Michigan into the MDNR's captive propagation program. Subsequent

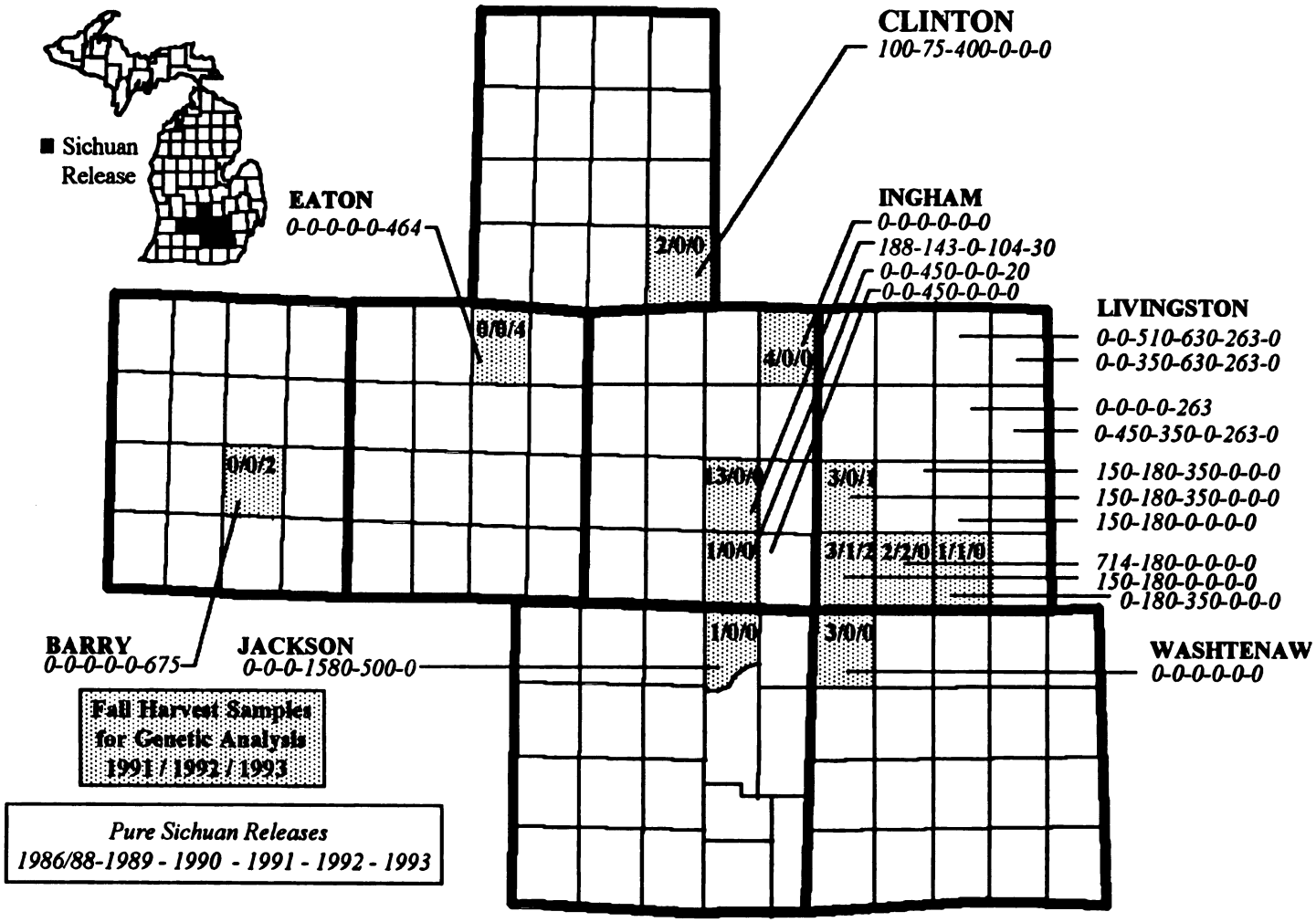

Figure 3. Townships (shaded) and number of free-ranging common pheasant males that were harvested in the fall for genetic analysis (1991-1993). The number of pure Sichuans released (1986-1992), and the townships (shaded and/or unshaded) into which they were released, are also noted.

hybrid, ring-neck, and back-cross releases were derived from crosses between the pure Sichuan and "wild" ring-necked captive breeding stocks.

Releases in Huron county included pure Sichuans, captive reared wild-trapped ring-necks from Michigan, Iowa, and North Dakota, F_1 hybrids (Sichuan x wild-trapped ring-neck), and various back-crosses. Locations of harvested and released birds were mapped by township for the Mixed release population (Fig. 4). Harvest locations for this study occurred in townships that had, or were next to, townships that had previously received release pheasants. The heritage of released pheasants in Huron county varied and most of the releases occurred on the western side of the county. Since 1986, 2,681 pheasants of Sichuan and/or ring-necked heritage have been released in 11 townships in Huron County. Pheasants were harvested in 11 townships, within which 7 (64%) had, or were adjacent to, townships that had previously received pheasant releases. The MDNR, in an attempt to reduce mortality, closed areas surrounding release sites to hunting making it difficult to sample release areas directly. Samples of free-ranging males pheasants from Huron County were collected as described above with the assistance of local Pheasant Forever Chapters.

Statistical Estimates

The allelic variation revealed by electrophoretic examination was analyzed using BIOSYS (Swofford and Selander 1989). The non-parametric Mann-Whitney U and Kruskal Wallis tests (Siegel 1956) were used to determine whether it was valid to increase sample sizes within the same site by pooling samples taken between pairs of years and within all years, respectively.

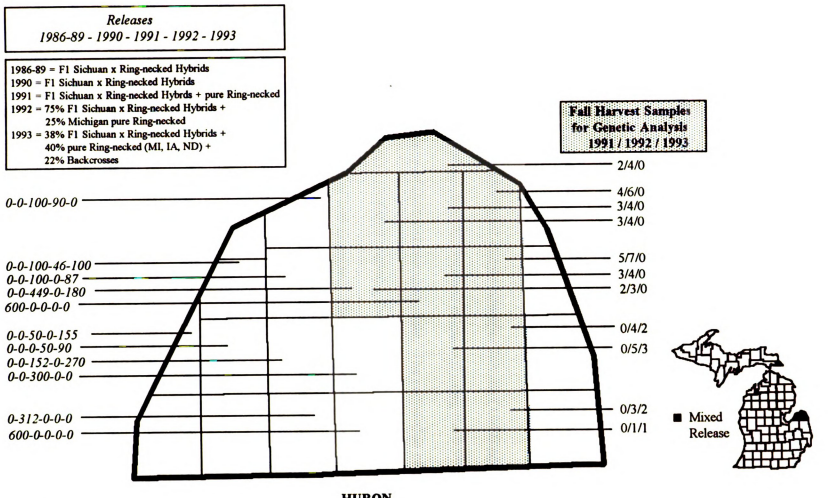

Figure 4. Townships (shaded) and the number of free-ranging common pheasant males harvested in the fall for genetic analysis (1991-1993). The number of birds of mixed heritage released (1986-1993), and the townships (shaded and/or unshaded) into which they were released, are also noted.

Genetic Heterogeneity

Allele and genotypic frequencies for each population were determined from the banding pattern on the gels. Mean observed, or direct count heterozygosity ($\bar{H}_{obs}$) , was calculated by determining the number of individuals heterozygous at a particular loci and dividing by the total number of individuals examined for that loci. This process was repeated for other loci and a mean estimate was obtained by averaging values over all loci. Mean expected heterozygosity ($\bar{H}_{exp}$) from the allele frequencies as if the population was in equilibrium was calculated as $1 - \sum_{i=1}^{n} \hat{p}_i^2$ where $\hat{p}_i$ is the frequency of the ith allele at a locus, with n alleles (Nei 1975). An unbiased estimate of $\bar{H}_{exp}$, based on conditional expectations, was corrected for small sample size after Levene (1949) and Nei (1978).

The percentage of polymorphic loci was calculated using the 0.99 and 0.95 criterion for the frequency of the most common allele. The proportion of polymorphic loci in the populations was calculated counting the number of polymorphic loci and then dividing by the total number of loci examined. Homogeneity in the number individuals carrying each allele in samples obtained from different sites was tested using the log-likelihood G-test (Sokal and Rohlf 1981).

Hardy-Weinberg Equilibrium:

For each polymorphic locus in each population, observed and expected genotypic frequencies were compared by the log-likelihood G-test to evaluate departure from Hardy-Weinberg equilibrium. Levene's (1949) correction for small samples size was used to calculate expected values.

Population Differentiation

The pattern of variation in allelic frequencies among populations was evaluated

using hierarchical F-statistics (Wright 1978). These statistics, F_{IS}, F_{ST} and F_{IT}, are related by the equation $(1 - F_{IS})(1 - F_{ST}) = (1 - F_{IT})$ (Wright 1965, 1978). The effects of population subdivision were measured by F_{ST}, the fixation index which varies from 0 to 1, and is the reduction in heterozygosity of a subpopulation due to random genetic drift. The inbreeding coefficient, F_{IS}, is the measure of reduction in heterozygosity of an individual due to nonrandom mating within a population. When positive, F_{IS} indicates matings between relatives occurs more often than would be expected if random, while a negative value indicates an avoidance of matings with relatives. F_{IT} is the most inclusive measure of inbreeding that takes into account both the effects of nonrandom mating within subpopulations and the effects of population differentiation (Hartel 1987).

Four methodologies were used to calculate genetic distance between pairs of populations: (1) Rogers (1972) distance (D_R), (2) Rogers (1972) distance as modified by Wright (1978) (D_W), (3) Nei (1978) unbiased genetic distance (D_N), and (4) Cavalli-Sforza and Edwards (1967) chord distance (D_C).

Rogers D_R was used because it is equivalent in principle to Mahalanobis' distance for morphological characters, so distances calculated from morphological and allelic data could be compared. It is also a simple observational measure with no assumptions. D_R is calculated using allele frequency data with one axis being used for each allele at the locus. When D_R equals zero, the two populations being compared are genetically identical, whereas if D_R equals unity, then the populations are fixed for different alleles. Therefore, the larger the value of D_R, the less 'related' are the populations. D_R is affected by the number of alleles. If multiple alleles are found in both populations, but none are held in common, then a distance that is a little less than 1 will be obtained. To calculate D_R over

several loci, the arithmetic mean of the D_R value at each locus is normally used.

Wright (1978) suggested it might be better to calculate the Euclidean distance over all loci by adding a dimension for every allele at every locus, (D_W), instead of taking an arithmetic mean as Rogers (1972) did. This gives less weight to loci in which the difference in allelic frequencies are small. To be an accurate estimate of distance in Euclidean hyperspace, each axis must be independent and on the same 'scale'. With genetic data, the 'scale' criteria is met, however the independent criteria is not for the frequency of all alleles at a locus must add up to unity. The failure to meet this assumption is routinely ignored.

Nei (1977) proposed a genetic distance measure based on a totally different concept to Rogers distance and begins with Nei (1972) standard distance (D). It is derived from the probability that 2 alleles, one drawn from each population unit being compared, are the same. The probability of picking the same allele from each population unit depends of the frequency of that allele in the 2 populations (i.e. $p_X \, x \, p_y$). If there are several alleles at a locus, then the chance of picking identical alleles is the sum of the probabilities of picking 2 copies of allele 1 plus the probability of picking 2 copies of alleles 2. The arithmetic mean is then taken over all loci. But, the probability of 2 alleles being identical when taken from the same population will be < 1 if there is polymorphism at the locus. Therefore a measure of distance between populations must take into account the amount of divergence within each of the populations. Nei gives a 'biological' meaning for D as an estimate of the number of DNA base differences per locus between populations.

Expanding on this concept, Nei (1978) suggested that genetic identity (I) could be

estimated as the normalized probability that 2 alleles, one taken from each population, are identical. It provides a measure of similarity in frequency of each alleles, summed over all alleles and the relationship between Nei's I and D is $D = -\log_e I$.

Nei (1978) also noted that estimates of genetic distance are systematically biased when sample sizes are small. To accommodate this, he replaced population gene identities with sample gene identities resulting in an unbiased estimate of genetic distance (D_N). The difference between biased (D) and unbiased (D_N) estimators of Nei's genetic distances is very small when the number of individuals is large (> 50).

Cavalli-Sforza and Edwards (1967) developed a measure of genetic distance which is Pythagorean in a Euclidian hyperspace, but which differs from Rogers (1972) concept in that it takes the square root of the allelic frequencies as the coordinates of the points representing the populations, instead of the frequencies themselves (Wright 1978). This locates all populations on the surface of a hyperspace such that all coordinates are non-negative. They all fall on the portion of this surface in which the coordinates of the point are non-negative. The chordal distance (D_C) is 0.9003 for populations with no allele in common. In determining chordal distances from multiple loci, the authors locate the population distances in a hyperspace with a dimension for each locus. The population coordinates along these are then equal to the chordal distances and thus not terminating on a hyperspace.

Patterns of population relatedness were examined by the unweighted pair-group method with arithmetic averaging (UPGMA) cluster analysis on the matrices of genetic distance for all methodologies, and Farris's (1972) distance Wagner network, optimized according to Swofford (1981) using Roger's (1972) distance as modified by Wright

(1978). Genetic distances using the methodology of Nei (1978) (D_N) was provided for comparison with the literature. Branching diagrams using D_R and D_C were provided for comparison with D_N. The "fits" of distances implied by the branching diagrams generated from genetic distances were evaluated by the F statistic of Prager and Wilson (1978). Their statistic is $F = 100 \sum_{i=1}^{n} |I_i - O_i| / \sum_{i=1}^{n} I_i$, where for n pair wise comparisons of populations, I and O are input values of the original matrix and the output values of the tree, respectively. Smaller values of F indicate greater congruence, but any $F < 0.10$ implies a good fit (Avise et al. 1982). The cophenetic correlation (r_{cc}) was also used to evaluate how well the resultant branching diagram represents the original distance matrix.

Cluster analysis using the UPGMA algorithm, was also performed first on the morphological data, (standardized neck ring closure and width), and then on the combination of standardized morphological and genetic (allele and genotype frequencies) of harvested males using PROC CLUSTER in PC-SAS (SAS Institute, Inc. 1993).

An alternative multivariate technique, principle component analysis, was used to examine the relationship among the populations. The purpose of principal component analysis is to derive a small number of linear combinations (principle components) of a set of variables that retain as much of the information in the original variables as possible (Rao 1964). Roger's (1972) distance as modified by Wright (1978) was used for comparison with the distance Wagner procedure.

An extensive literature review of protein electrophoresis studies dealing with avian species was performed. Observed (direct count) and expected (Nei's (1978) unbiased estimate) heterozygosity (Appendix C), and Nei (1978) unbiased genetic distance and Wright's (1978) F_{ST} (Appendix D) were recorded for comparison with this study.

RESULTS

Genetic Variability

Captive F_1 Sichuans, obtained either from the breeding stock directly or from individuals selected for release, showed similar allele frequencies (Mann-Whitney U, z = -0.484, P = 0.613, df = 1) (Appendix B). Allele frequencies were similar between pheasants from Hillsdale and Montcalm counties in 1991 (Appendix B) (Mann-Whitney U, z = -0.721, P = 0.471, df = 1) and there was no significant difference among years within the ring-necked individuals (Kruskal-Wallis, T = 0.061, P = 0.970, df = 2) (Appendix B). Allele frequencies (Appendix B) were similar among years within mixed release (KW, T = 0.143, P = 0.931, df = 2 and the Sichuan release population (KW, T = 0.319, P = 0.853, df = 2). Since no significant differences were noted between sites and among years, data on the 192 individuals were pooled for the 6 loci within the Captive Sichuan, ring-necked, Pure Sichuan Release, and Mixed Release populations (Table 5).

Allele frequencies were determined for all 4 combined populations (Table 6). Allele frequencies of ACON-2 were similar between the Captive Sichuan, Mixed Release, and Sichuan release populations, which were collectively different from the ring-necked population. Log-likelihood G values indicated a significant difference in the number of individuals carrying each allele for all loci except ACP (Table 7).

For each population, direct counts were made of the proportion of heterozygous individuals per locus. When averaged across the 30 assayed loci, the resulting heterozygosity ($\bar{H}_{obs}$) ranged from 0.019 in the Sichuan Release population to 0.029 in the Captive Sichuan population (Table 8). $\bar{H}_{exp}$ ranged from 0.035 to 0.042 for the Sichuan Release and Captive Sichuan populations, respectively. Heterozygosity levels observed in

this study were slightly lower than those published for other *Phasianus* ($\bar{H}_{obs}$ = 0.041 ± 0.007 SE, n = 5, range 0.026 - 0.066) and other galliformes ($\bar{H}_{obs}$ = 0.040, n = 18, range 0.000 to 0.083) (Appendix C). Percentage of loci polymorphic was similar across all 4 populations.

Genotypic frequencies varied between populations (Table 9). G values (Table 10) generated from testing for homogeneity between the observed and the expected number of genotypes indicated that the captive Sichuan population was in Hardy-Weinberg equilibrium, whereas the three release populations were not. Average F_{IS} was -0.114 across populations and all loci except ACP were negative indicating an avoidance of matings with relatives (Table 11). An average F_{ST} of 0.298 (0.000 to 0.718) was observed suggesting that 70% of the total genetic variation is found within populations, while 30% is distributed among populations (Table 11).

Table 5. Sample sizes, by loci, for 4 populations of common pheasants in southern Michigan used for genetic analysis. Captive pheasants were collected from 1990-92 while free-ranging pheasants were collected from 1991-1993.

Loci	Captive[a]	Free-ranging			Total
		w/o releases	with releases		
	Sichuan	Ring-necked[b]	Mixed[c]	Sichuan[d]	
ACP	37	49	60	45	191
AP	35	46	59	45	185
IDH-1	35	47	59	45	186
IDH-2	35	48	60	45	188
ACON-1	35	48	61	45	189
ACON-2	37	48	62	45	192[e]

[a] samples from MDNR's captive breeding stock of Sichuan pheasants at the Mason Wildlife Facility (1990-92)
[b] samples from Hillsdale (1991-93) and Montcalm (1991) counties
[c] samples from Huron County (1991-93)
[d] samples from Livingston (1991-93), Jackson (1991), Ingham (1991), Washtenaw (1991), Barry (1992-93), Clinton (1992), & Eaton (1993) counties
[e] maximum number of individuals sampled

Table 6. Allele frequencies of common pheasants collected for genetic analysis from 4 populations in southern Michigan. Captive pheasants were collected from 1990-92, while free-ranging pheasants were collected from 1991-1993.

Loci	Allele	Captive	Free-ranging		
			w/o releases	w/releases	
		Sichuan[a]	Ring-necked[b]	Mixed[c]	Sichuan[d]
ACP	a	0.892	0.827	0.902	0.891
	b	0.108	0.173	0.098	0.109
AP	a	0.643	0.772	0.517	0.859
	b	0.357	0.228	0.483	0.141
IDH-1	a	0.843	0.750	0.692	0.913
	b	0.157	0.250	0.308	0.087
IDH-2	a	0.971	1.000	0.852	1.000
	b	0.029	0.000	0.148	0.000
ACON-1	a	0.886	0.260	0.379	0.337
	b	0.114	0.740	0.621	0.663
ACON-2	a	0.947	0.117	0.881	0.989
	b	0.054	0.883	0.119	0.011

[a] samples from MDNR's captive breeding stock of Sichuan pheasants at the Mason Wildlife Facility (1990-92)
[b] samples from Hillsdale (1991-93) and Montcalm (1991) counties
[c] samples from Huron County (1991-93)
[d] samples from Livingston (1991-93), Jackson (1991), Ingham (1991), Washtenaw (1991), Barry (1992-93), Clinton (1992), & Eaton (1993) counties

Table 7. G values generated from the analysis of homogeneity in the number of individuals carrying each allele, by loci, for each population (df = 1) and combined populations (df = 3) of common pheasants collected for genetic analysis in southern Michigan.

Locus	Captive	Free-ranging			Combined
	Sichuan	w/o release	with release		
		Ring-necked	Mixed	Sichuan	
ACP	0.803	0.983	0.403	0.108	2.99
AP	0.312	1.622	7.551**	7.270**	33.51***
IDH-1	1.014	0.467	3.248	5.037*	19.54***
IDH-2	0.484	5.191*	7.576**	4.974*	36.45***
ACON-1	31.690***	6.084*	0.715	1.733	80.45***
ACON-2	11.604***	79.137***	8.277**	24.050***	246.14***

*$P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.005$

Table 8. Genetic variability (± SE) in 6 loci for populations of common pheasants collected for genetic analysis in southern Michigan.

Population	mean no. of alleles per locus	percentage of loci polymorphic		mean heterozygosity	
		.95[a]	.99[b]	DC[c]	unbiased[d]
Captive					
Sichuan	1.19	16.13	19.35	0.029	0.042
	(0.07)			(0.014)	(0.019)
Free-ranging					
Ring-necked	1.16	16.13	16.13	0.020	0.052
	(0.07)			(0.009)	(0.022)
Mixed Releases	1.19	19.35	19.35	0.023	0.066
	(0.07)			(0.011)	(0.027)
Sichuan Releases	1.16	12.90	16.13	0.019	0.035
	(0.07)			(0.009)	(0.018)

[a] the frequency of the most common allele is 0.95; [b] the frequency of the most common allele is 0.99; [c] DC = direct count; [d] unbiased estimate of Nei (1978)

Table 9. Genotypic frequencies of common pheasants collected for genetic analysis from 4 populations in southern Michigan. Captive pheasants were collected from 1990-1992, while free-ranging pheasants were collected from 1991-1993.

Loci	Genotype	Captive	Free-ranging		
			w/o releases	with releases	
		Sichuan[a]	Ring-necked[b]	Mixed[c]	Sichuan[d]
ACP	aa	0.84	0.78	0.84	0.83
	ab	0.11	0.10	0.13	0.13
	bb	0.05	0.12	0.03	0.04
AP	aa	0.49	0.74	0.45	0.80
	ab	0.31	0.06	0.13	0.11
	bb	0.20	0.20	0.42	0.09
IDH-1	aa	0.74	0.64	0.58	0.85
	ab	0.20	0.21	0.22	0.13
	bb	0.06	0.15	0.20	0.02
IDH-2	aa	0.97	1.00	0.85	1.00
	ab	0.00	0.00	0.00	0.00
	bb	0.03	0.00	0.15	0.00
ACON-1	aa	0.80	0.19	0.27	0.24
	ab	0.17	0.14	0.21	0.20
	bb	0.03	0.67	0.52	0.56
ACON-2	aa	0.92	0.06	0.87	0.98
	ab	0.05	0.11	0.02	0.02
	bb	0.03	0.83	0.11	0.00

[a] samples from MDNR's captive breeding stock of Sichuan pheasants at the Mason Wildlife Facility (1990-92)
[b] samples from Hillsdale (1991-93) and Montcalm (1991) counties
[c] samples from Huron County (1991-93)
[d] samples from Livingston (1991-93), Jackson (1991), Ingham (1991), Washtenaw (1991), Barry (1992-93), Clinton (1992), & Eaton (1993) counties

Table 10. G values, (df = 1), generated from testing for homogeneity between the observed number of genotypes and the Hardy-Weinberg expected number of genotypes, for the 4 populations of common pheasants collected in southern Michigan for genetic analysis.

Locus	Captive	Free-ranging		
		w/o releases	with releases	
	Sichuan	Ring-necked	Mixed	Sichuan
ACP	1.36	16.15***	0.80	0.99
AP	3.45	28.38***	36.00***	9.49***
IDH-1	1.16	8.67**	14.12***	-1.04
IDH-2	1.97	fixed	51.10***	fixed
ACON-1	-0.90	17.37***	19.61***	14.54***
ACON-2	-0.74	4.81	35.00***	-0.01

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$; for 1-tail test

Table 11. Summary of hierarchial F-statistics (Wright 1965, 1978) at all polymorphic loci in southern Michigan common pheasants. Significance levels are associated with Chi-square tests of (1) H_o: $F_{IS} = 0$, and (2) H_o: $F_{ST} = 0$; * $P < 0.05$, ** $P < 0.01$.

Locus	F_{IS}[a]	F_{IT}	F_{ST}[b]
ACP	0.001	0.001	0.000
AP	-0.079	0.069	0.137**
IDH-1	-0.048	0.038	0.082**
IDH-2	-0.046	0.080	0.120**
ACON-1	-0.151*	0.236	0.336**
ACON-2	-0.268**	0.651	0.718**
Combined	-0.114	0.218	0.298**

[a] Chi-square = $F_{IS}^2 N(k\text{-}1)$, df = $[k(k\text{-}1)]/2$ (Waples 1987), where N is the total number of individuals sampled from populations polymorphic for the locus being tested, and k is the number of alleles at that locus.

[b] Chi-square = $2NF_{ST}(k\text{-}1)$, df = $(k - 1)(s - 1)$ (Waples 1987), where N and k are defined as above, and s is the number of populations polymorphic for the locus being tested.

Genetic Distance

Genetic distances between the 4 populations of common pheasants in southern Michigan were small. Rogers (1972) (D_R) and Roger's distance as modified by Wright (1978) (D_W) (Table 12), along with Nei's (1978) unbiased genetic distance (D_N) (Table 13) are presented for comparison to other studies of this type. Average distances ranged from 0.019 (D_N, 0.006-0.038, n = 6 comparisons) to 0.132 (D_W, 0.081-0.189, n = 6). Wright's modification of Rogers (1972) distance resulted in a larger estimate. Cavalli-Sforza and Edwards distances (D_c = 0.101, 0.076-0.137, n = 6) (Table 13) were intermediate. In all cases, individuals from Captive Sichuan and free-ranging ring-necked populations were identified as having the greatest genetic distance. Free-ranging Sichuan and Mixed Release populations were intermediate.

The branching diagrams for all distance measures indicate similar patterns regardless of the genetic distance index used (Figs. 5-9). The distance Wagner tree, generated from Roger's (1972) distance as modifed by Wright (1978) (Fig. 9) showed the best fit (F = 0.917, r_{cc} = 0.998) compared to the other diagrams. Although the branching diagram based on Nei's (1978) unbiased genetic distance (Fig. 7) had a high F value (F = 15.313), the cophenetic correlation indicates the diagram represents the original distance matrix (r_{cc} = 0.921). Relative distances between populations generated from the first 2 principle coordinates (Fig. 10) indicates a pattern similar to those seen in the UPGMA branching diagrams using genetic distances.

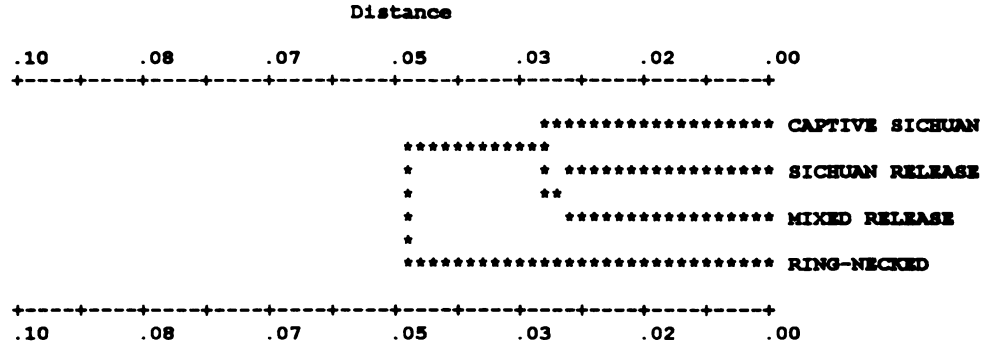

Figure 5. UPGMA branching diagram based on Rogers (1972) genetic distance (D_R) representing the variation between the 4 populations of common pheasants found in southern Michigan., F = 9.306, r_{cc} = 0.878.

Table 12. Genetic distance matrix summarizing the genetic variance found in 4 populations of common pheasants in southern Michigan. Above the diagonal Rogers (1972) genetic distances (D_R); below the diagonal are Rogers (1972) genetic distances as modified by Wright (1978) (D_W).

Population	1	2	3	4
1 Captive Sichuan	---	0.057	0.032	0.029
2 Ring-necked	0.189	---	0.046	0.041
3 Mixed Release	0.101	0.150	---	0.028
4 Sichuan Release	0.107	0.161	0.081	---

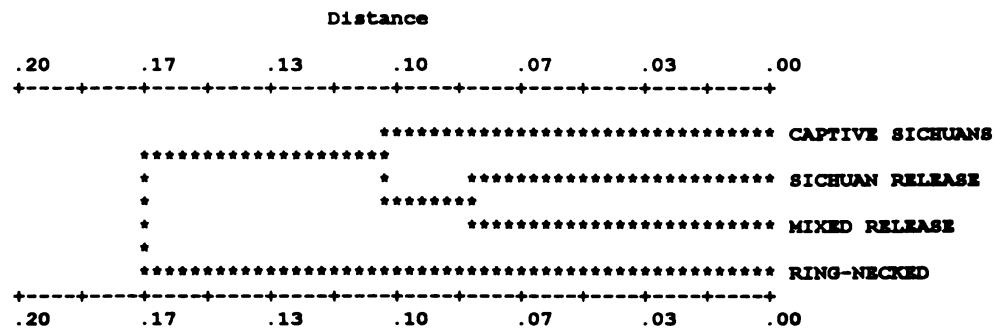

Figure 6. UPGMA branching diagram based on Rogers (1972) distance as modified by Wright (1978) (D_W) representing the variation between the 4 populations of common pheasants in southern Michigan, F = 6.405, r_{cc} = 0.950.

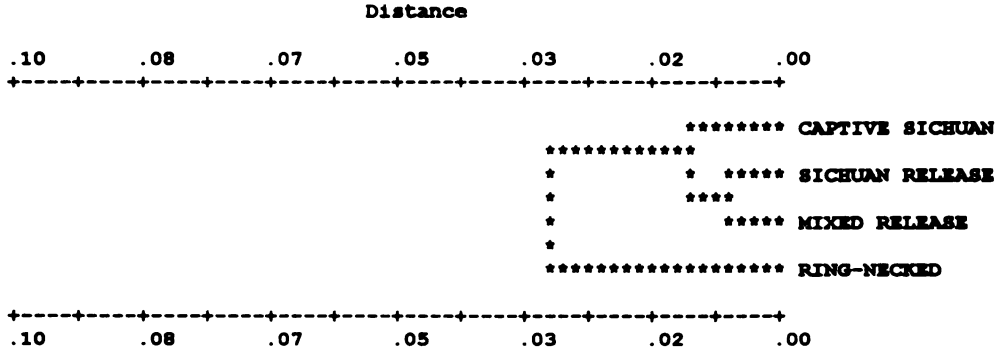

Figure 7. UPGMA branching diagrams based on Nei (1978) unbiased genetic distance (D_N) representing the variation between the 4 populations of common pheasants found in southern Michigan, F = 15.313, r_{cc} = 0.921.

Table 13. Genetic distance matrix summarizing the genetic variance found in common pheasants in southern Michigan. Above the diagonal are Neis (1978) unbiased genetic distances (D_N); below the diagonal are Cavalli-Sforza and Edwards (1967) chord distances (D_C).

Population	1	2	3	4
1 Captive Sichuan	---	0.038	0.010	0.011
2 Ring-necked	0.137	---	0.023	0.027
3 Mixed Release	0.075	0.113	---	0.006
4 Sichuan Release	0.079	0.125	0.076	---

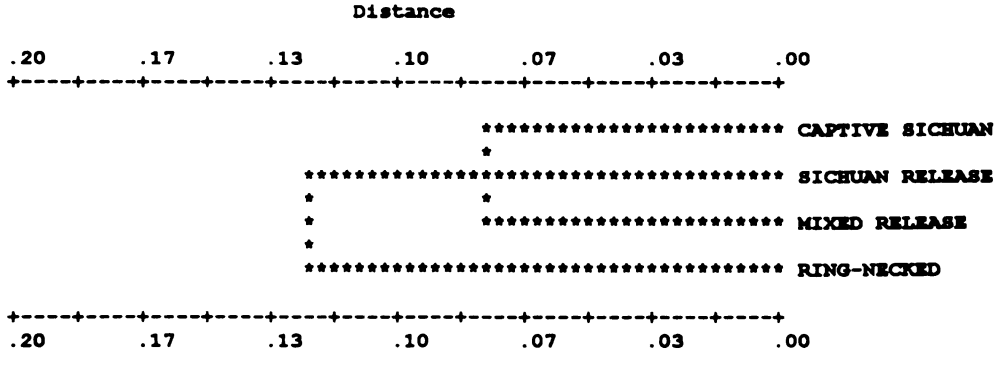

Figure 8. UPGMA branching diagram based on Cavalli-Sforza and Edwards (1967) chord distance (D_C) representing the variation between the 4 populations of common pheasants in southern Michigan, F = 4.503, r_{cc} = 0.960.

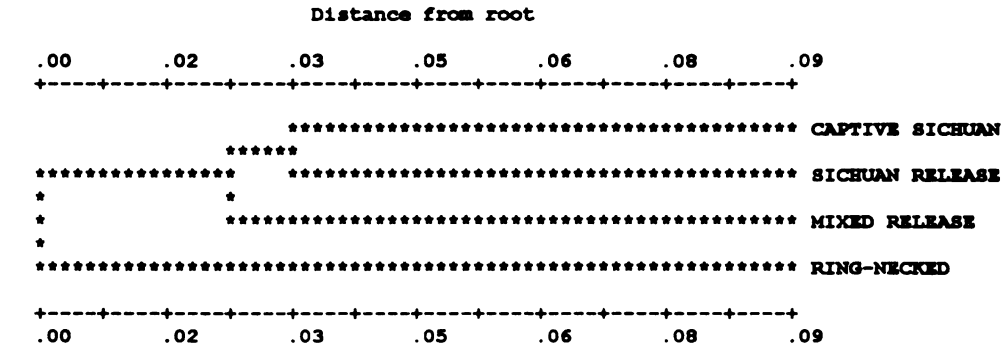

Figure 9. Distance Wagner tree showing the association of 4 populations of common pheasants in southern Michigan generated from Rogers (1972) distance as modifed by Wright (1978). Total length of tree = 0.263, F = 0.917, r_{cc} = 0.998.

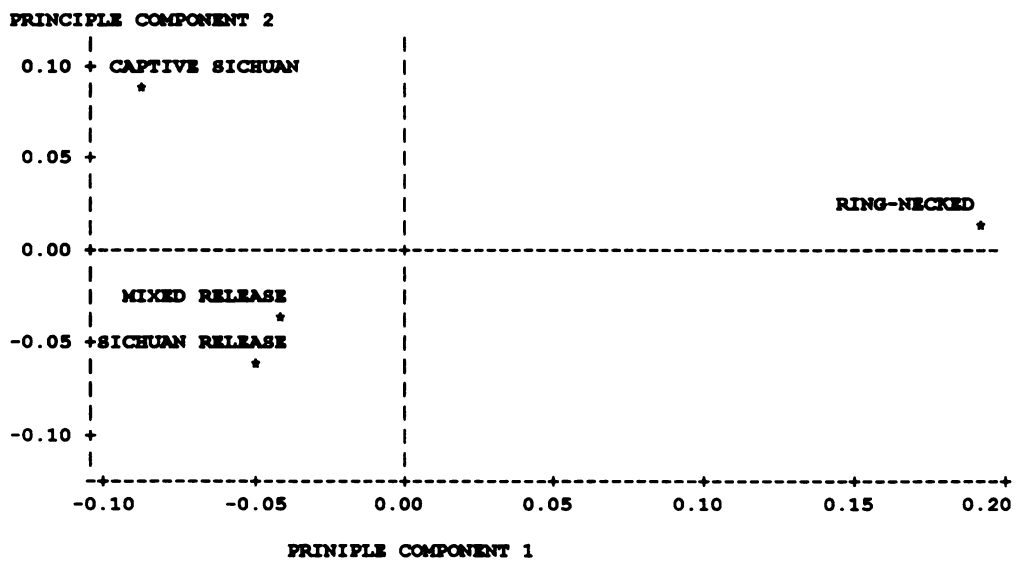

Figure 10. Relative genetic distances of the 4 populations of common pheasants found in southern Michigan, plotted by the first 2 principle coordinates. Distance measure used was Rogers (1972) distance as modified by Wright (1978).

Neck ring width and percent closure data of sampled males are presented in Table 14. Captive Sichuans did not possess a neck ring. Neck rings of hybrid males were intermediate between the races and ranged from white spots to a narrow white ring. Although neck ring width was the greatest in the ring-necked population, it was not significantly different from the Mixed (Mann-Whitney U test, $z = 0.3328$, $P = 0.7393$) or the Sichuan release ($z = -0.9784$, $P = 0.3279$) populations. Closure of the neck ring was similar between the ring-necked and Mixed populations ($z = 0.2835$, $P = 0.7768$). However, neck ring closure in the Pure Sichuan Release population was significantly more open than the ring-necked ($z = 3.9337$, $P = 0.001$) and Mixed release ($z = 3.8291$, $P = 0.001$) populations. UPGMA clustering using standardized neck ring width and closure separated the captive Sichuan population from the others (Fig. 11). Separation remained using UPGMA clustering on morphological, allelic, and genotypic data resulted in a pattern similar to that seen with the genetic distance meaures where Captive Sichuan and release populations clustered together (Fig. 12).

Table 14. Average neck ring width ± SE and percent neck ring closure of males harvested in the fall for genetic analysis from 4 populations of pheasants in southern Michigan.

Neck ring	Captive	Free-Ranging		
	Sichuan[a]	w/o releases	w/releases	
		Ring-necked[b]	Mixed[c]	Sichuan[d]
% of indivs. showing a ring	0	100	100	95
width (mm)	NA	20.83	18.87	18.94
± SE		1.0	0.07	1.1
n		40	47	39
% closure	NA	.90	0.92	0.80
± SE		0.7	1.0	0.0
n		49	52	39

[a] samples from MDNR's captive breeding stock of Sichuan pheasants at the Mason Wildlife Facility (1990-92)(n = 30)
[b] samples from Hillsdale (1991-93) and Montcalm (1991) counties
[c] samples from Huron county (1991-93)
[d] samples from Livingston (1991-92), Jackson (1991), Ingham (1991), Washtenaw (1991), Barry (1992-93), Clinton (1992) and Eaton (1993) counties
NA = not applicable

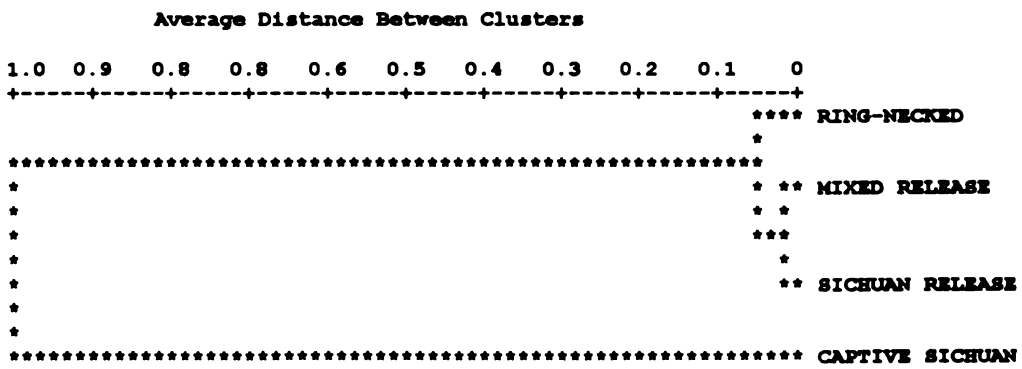

Figure 11. UPGMA cluster analysis using standardized morphological data from the 4 populations of common pheasants in southern Michigan.

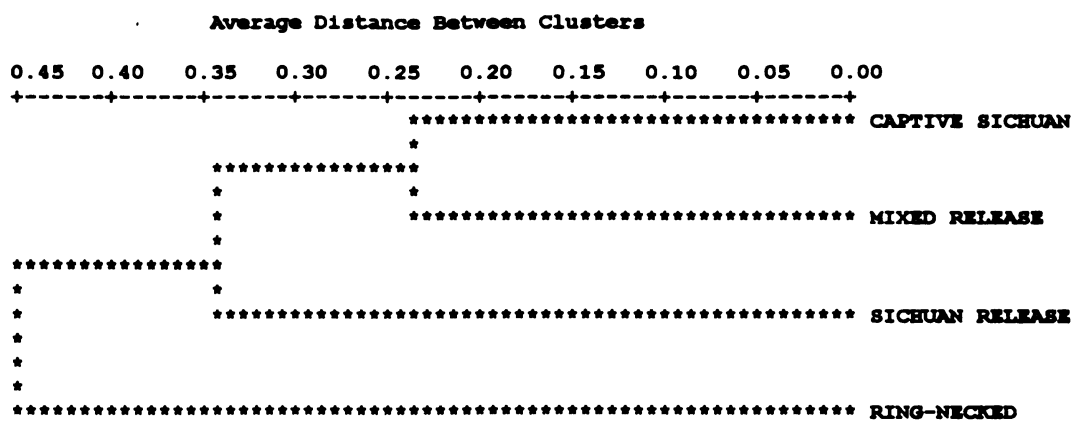

Figure 12. Cluster analysis, using UPGMA methodology on standardized morphological, allelic, and genotypic frequencies for the 4 populations of common pheasants in southern Michigan.

DISCUSSION

Levels of genetic heterogeneity and differentiation were estimated between populations of common pheasants in southern Michigan that areSichuan, ring-necked and a mixture of Sichuan and ring-necked hybrids. The free-ranging ring-necked population represents the pheasant gene pool that remains in Michigan from more than 40 years of releases by the Michigan DNR (1919 to 1950's). Also included in this gene pool were continuous, unmonitored introductions by release and/or escape of game farm ring-necked pheasants each year by private individuals and organizations. The free-ranging Sichuan gene pool was from the captive breeding population of Sichuan pheasants. Electrophoretic screening of samples of individuals provided allele frequencies, from which estimates of genetic structure could be made, which are concordant with those based on demographic modeling (Barrowclough 1980a). The biochemical methods also yielded information on the magnitude and distribution of genetic heterozygosity and polymorphism (Barrowclough 1983).

Genetic Heterogeneity

Little difference was noted in the levels of polymorphism in the Captive Sichuan and free-ranging populations. However, the polymorphism is an imprecise measure of genetic variability as a slightly polymorphic locus has as much weight as a very widely polymorphic one, and the accuracy of this estimate depends on the number of loci examined (minimum of 14, 20 recommended) and the number of individuals (minimum of 30, recommended 100) (Evans 1987). This survey, as well as those of other wild galliformes (Gutierrez et al. 1983, Warner et al. 1988, Scribner et al. 1989) often survey more than the suggested number of loci, but fail to survey the recommended number of individuals.

Probably the most widespread measure of genetic variation used to describe genetic variability in populations is the level of heterozygosity (Evans 1987). Although average observed heterozygosity ($\bar{H}_{obs}$) in the ring-necked and captive Sichuan populations in this study were similar (2% and 2.9%, respectively), both were slightly lower than values reported in the literature for other avian species (Appendix C). Average observed variability in five other *Phasianus* studies was 4.1%. Within the subfamily Phasianinae, values averaged 4.8% (0-8.3%, n = 18 studies). Many avian surveys typically have very low levels of within species genetic variation. (Barrowclough 1980a).

The deficiency of heterozygotes in common pheasant populations in Michigan is also reflected in the negative values observed for the inbreeding coefficient, F_{IS}. Negative F_{IS} values are thought to indicate a general avoidance of matings with relatives. Values of F_{IS} in this study averaged -0.114 (-0.238 to 0.001) and were similar to those found in wintering populations of brant (*Branta bernicla hrota*) (-0.126 to -0.012) (Novak et al.

1989), and Florida wood storks (*Mycteria americana*) (-0.091) (Stangel et al. 1990). Generally, avian populations show a tendency toward matings with relatives (Table 15).

The majority of the loci in the free-ranging pheasant populations in Michigan were not in Hardy-Weinberg equilibrium, while all loci in the Captive Sichuans were in equilibrium. However, there were three loci, (ACP, IDH-1, and ACON-2) in equilibrium in the Sichuan Release population, compared with only one loci (ACP) in the Mixed Release population and none in the non-release ring-necked population. It is possible that the pure releases had positively influenced levels of heterozygosity in the free-ranging

Table 15. A summary of literature F_{IS} values in the Class Aves.

Common Name	Scientific Name	F_{IS}	Source
yellow-rumped warbler	*Dendroica coronata*	0.08	Barrowclough 1980b
northern oriole	*Icterus galbula*	0.312	Corbin et al. 1979
piping plover	*Charadrius melodus*	0.049	Haig and Oring 1988
brant	*Branta bernicla hrota*	-0.126 to -0.012	Novak et al. 1989
American wigeon	*Anas americana*	0.046	Rhodes et al. 1993
starling	*Strunus vulgaris*	0.040	Ross 1983
willow flycatcher	*Empidonax traillii*	-0.025	Seutin and Simon 1988
alder flycatcher	*E. alnorum*	0.063	Seutin and Simon 1988
white headed gulls	*Larus* spp.	0.081	Snell 1991
Florida wood stork	*Mycteria americana*	-0.091	Stangel et al. 1990
California quail	*Callipepla californica*	0.130	Zink et al. 1987
ring-necked pheasant	*Phasianus colchicus*	0.130	Scribner et al. 1989
ring-necked pheasant	*P. colchicus*	-0.114	This study

populations, and pure Sichuan releases had the greatest impact since they were in Hardy-Weinberg equilibrium.

In a non-equilibrium population, the observed heterozygosity may not accurately reflect the amount of genetic variation in the population, and to deal with this problem, it is advised that the expected heterozygosity be calculated (Evans 1987). The difference between observed and expected heterozygosity was 2 times greater for populations not in equilibrium compared with those at or near equilibrium. Average expected heterozygosity in common pheasants in southern Michigan (0.035-0.066) was similar to values reported within the Subfamily Phasinidae ($\bar{H}_{exp} = 0.048 \pm 0.02$, n = 2) (Appendix C).

The low proportion of heterozygotes found in common pheasants in Michigan may have resulted from a variety of factors including assortative mating, small population sizes, and/or biased sampling. The pheasant is a polygynous species and males will mate with a limited number of females within a defined territory (Taber 1949). Research in Michigan indicates that average summer home range size of Sichuan and ring-necked males released in Livingston County, Michigan, ranged from 67.4 to 100.2 ha, respectively (Campa 1989). Aggressive behavior between males of both races was observed in the field (Campa et al. 1987) suggesting an overlap of territories. Grahn et al. (1993) estimated harem size at 1.3 ± 1.0 SD hens per day for pheasants in Sweden under controlled conditions and DNA fingerprinting revealed that males sired an average of 6.0 ± 1.01 SD chicks from a total of 17 broods (approximately 102 chicks). The lack of males in the fall harvest without neck-rings in this study suggests almost no breeding between pure free-ranging Sichuan males and females. It is likely that hens had the opportunity to select between males in the field.

Allele frequencies under complete positive assortative mating will not change from generation to generation, but the genotypic proportions will change considerably (Li 1955). If H_n is the proportion of heterozygotes in a population at time n, and p is the frequency of the A allele (which will be the same for both parental and offspring; see Li (1955) pg 233), then heterozygotes in the next generation (H_{n+1}) under complete positive assortative mating will be reduced by: $H_{n+1} = [2pH_n] / [2p + H_n]$ (Li 1955). If assortative mating continues for n generations, and H_o and p are the values from the parental generation, then: $H_n = [2pH_o] / [2p + nH_o]$ and H_n approaches zero as n increases.

It would take 0.6 to 4.4 generations to achieve the 0.1% reduction in observed heterozygosity based on the average observed heterozygosity ($\bar{H}_{obs}$) estimates from the ring-necked ($H_o = 0.020$) and Sichuan Release ($H_n = 0.019$) populations. Estimates range from 2.2 to 15.4 generations if expected heterozygosity ($\bar{H}_{exp}$) is used. These estimates assume that the existing remnant ring-necked population within the Sichuan release population was substantial and genetically similar to our sampled ring-necked population, and complete positive assortative mating occurred between existing and released birds.

The lower observed heterozygosity estimates of free-ranging populations in this study (0.019 to 0.023) may also depend on neighborhood size. If population dispersion is uniform, neighborhood size (N_e) can be estimated by $N_e = 4\ \pi\delta\sigma^2$ where δ is the number of breeding individuals/unit area, and σ^2 is the amount of dispersion between an individual's birth place and that of its offspring. Luukkoneon (1991) estimated wintering population densities of pheasants at 16.9 birds/ km^2 in Livingston County (1574 pheasants / township). Dispersion estimates between a breeding individual's birth place and that of

its offspring are not available for pheasants, however they can be approximated by using the distances females disperse from release to nesting sites and between nesting attempts (mean = 3.9 km) (Prince et al. 1986, Campa et al. 1987, Rabe et al. 1988, Campa 1989). Substituting the winter population estimates for δ and dispersal distances for σ^2, results in a neighborhood size for pheasants in Livingston County of 3234 pheasants (4π * 16.9 birds/km^2 * 15.2 km^2). If pheasant densities remained at 16.9 birds/km^2 throughout the sampling period, an area equivalent to 2 townships should have been sampled. Since 4 townships were sampled in Livingston County, the possibility of sampling more than one neighborhood exists. This could lead to disequilibrium condition if allele differences existed between neighborhoods.

The deficiency in heterozygosity, resulting from combining within a single sample, individuals from more than one genetically distinct population is known as the Wahlund effect (Wahlund 1928) and the outcome is similar to inbreeding (Li 1955). The Wahlund effect, for a particular allele at some locus, is the expected deficiency of heterozygotes in a non-interbreeding mixture of two populations. It is expressed as: $\bar{H}_{obs} - \bar{H}_{exp} = -2f_1f_2(p_1 - p_2)^2$, where $\bar{H}_{obs}$ and $\bar{H}_{exp}$ are the observed and expected frequencies of heterozygotes, f_1 and f_2 are the proportional contributions of populations 1 and 2 to some mixture ($f_1 + f_2 = 1$), and p_1 and p_2 are the frequencies of the alleles in populations 1 and 2, respectively. The difference between observed and expected heterozygosity will be $\leq$ zero and will equal zero only if allele frequencies in the two populations are identical ($p_1 = p_2$). The difference is maximized when the two populations present in the mixture are in equal proportions ($f_1 = f_2 = 0.5$) (Ryman and Utter 1987). If local populations with different allelic frequencies are sampled, then the mixture of individuals from the various

populations could result in an apparent overall excess of homozygotes even if each local population is in equilibrium.

The effect of assortative mating and small neighborhood size on levels of heterozygosity in Michigan pheasants may have overridden the selective benefit of heterozygosity Niewoonder (1995) documented in the survival of hybrid females. Sichuan x ring-necked hybrid females in southern Michigan had slightly higher survival and produced 2 to 4 times more chicks/hen/season compared with Sichuan and ring-necked females, respectively. Heterosis in F_1 crosses is possible if allele frequencies differ between the crossed lines, however hybrid vigor is expected to halve in the F_2 progeny (Falconer 1989).

Population Differentiation

Gene flow from the captive Sichuan into the release populations appeared to be substantial as evidenced by the genetic identity measures. In all indices, the release populations were intermediate to the pure Captive Sichaun and free-ranging ring-necked populations. This is supported by other evidence that assortative mating between ring-necked and Sichuan pheasant is not complete. Prince et al. (1991) found evidence of positive assortative mating when wild-trapped Michigan ring-necked hens were given the opportunity to select between ring-necked and Sichuan males under controlled conditions. Ring-necked hens mated more frequently with ring-necked (80%) compared with Sichaun males (20%). In a reciprocal experiment, Sichuan females mated with ring-necked and Sichuan males at a similar frequency (48% and 52%, respectively).

The biochemical markers were more useful in distinguishing the various populations than the morphological marker. Pure Sichuans had no ring, but both the pure

and mixed free-ranging populations had rings similar to the ring-necked population. Plumage patterns are the product of regulatory genes and may not mirror patterns found in structural genes that code for proteins. Pleiotropy or complex genetic-environmental interactions during ontogeny are reduced by biochemical methods. Therefore, biochemical characters may be "cleaner" than are phenotypic ones (Barrowclough 1983). Differences between branching diagrams based on genetic distances to those based on phenotypic variables suggest caution in the interpretation of the relationship between groups based on phenotypic characters alone.

The utility of phenological traits in differentiating species and subspecies has been highly variable. Barrowclough (1980b) did find sufficiently strong phenotypic differentiation within a zone of hybridization between *Denrocia c. coronata* and *D. c. auduboni* where the two forms were originally thought to be separate species. However, his analysis of the genetic data indicated no differentiation among populations ($D_N = 0.006 \pm 0.002$). Johnson and Marten (1992) found considerable concordance of morphometric (body size) and genetic patterns in a subspecies of sage sparrow (*Amphispiza belli*). However, Lougheed and Handford (1992) found no discernable relationship between the pattern of trill rate variation (dialects) and genetic population structure in rufous-collared sparrows (*Zonotrichica capensis*) in northwestern Argentina, and Zink (1982) measured 40 skeletal characters in the rufous-collared sparrow and 4 other congeners and found genetic divergence without concomitant morphological change. While documenting patterns of phenotypic variation is useful because they may provide general indications of evolutionary trends, genic evolution can occur without concomitant morphological change (Gorman and Kim 1977, Highton and Larson 1979), and organisms with different

morphologies may be even be genetically similar (Avise et al. 1975, King and Wilson 1975, Yang and Patton 1981).

While the biochemical markers were more useful than size of the neck-ring in distinguishing the populations of pheasants in Michigan, levels of differentiation were much lower than most other animal species. They were, however, in the range generally found for avian species. Literature values of Nei's unbiased genetic distance for between subspecies and between local populations averaged 0.013 ± 0.016 ($n = 10$) and 0.002 ± 0.016 ($n = 6$), respectively (Appendix D). The differences for Michigan pheasants ranged from 0.006 to 0.038. The values of D_N measured in this study were more similar to those reported for comparisons between avian subspecies than for local populations of the same species (Fig. 13).

In spite of their high levels of genetic identity, the populations of common pheasants in Michigan showed substantial differentiation using Wright's (1965, 1978) hierarchical F-statistics. Wright (1978) defines F_{ST} as the correlation between alleles of gametes sampled at random from two subdivisions of a population, with the distribution of alleles within the entire population sampled. Therefore, F_{ST} reflects the extent of local differentiation into subpopulations or demes and is always positive. Wright (1978) described four ordinal levels of F_{ST}, 1) little genetic differentiation ($F_{ST} = 0$ to 0.05), 2) moderate (0.05 - 0.15), 3) great (0.15 - 0.25), and 4) very great (> 0.25). The average F_{ST} of 0.298 (0.000 to 0.718)in the common pheasants of Michigan indicates a large amount of differentiation between populations.

Distributions of interpopulational values of F_{ST} have been summarized for several groups of organisms (Barrowclough 1983, Corbin 1983, 1987). For vertebrates,

interdemic F_{ST} values range between 0.0 to 0.91, with the largest values being found among salamander populations. The value of F_{ST} for populations of common pheasants in southern Michigan is 10 fold greater than that previously described among avian populations where the largest interdemic F_{ST} values have been reported between 0.029 to 0.039 (Corbin 1987).

In other pheasant work, Scribner et al. (1989) found in Texas Panhandle populations (n = 10) derived from *P c. bianchi*, *P. c. torquatus*, and *P. c. colchicus*, that 91% of the genetic variance was found within populations (F_{ST} = 0.086). The patchy distribution of playa basin habitat in the Texas Panhandle, coupled with large interplaya distances were suggested causes for spatial structuring over a short post-introduction period. The average F_{ST} value for populations of common pheasants in Michigan (0.298) is 3 ½ fold greater than that seen by Scribner et al. (1989). Differences in stocking history and population densities could account for part of this difference, as the heritage of pheasants in Texas was similar to that of Michigan's current ring-necked population. Introductions of the Sichuan pheasant, a subspecies new to North America, contributed to the increase in differentiation seen in Michigan populations. Pheasant populations in Texas were considered quite large and averaged 40 birds/km^2 (Guthery and Whiteside 1984), a density 2 ½ that of Michigan populations (16.9 birds/km^2) (Luukkoneon 1991). The effect of genetic drift is greater in smaller populations and may result in a greater degree of differentiation between populations.

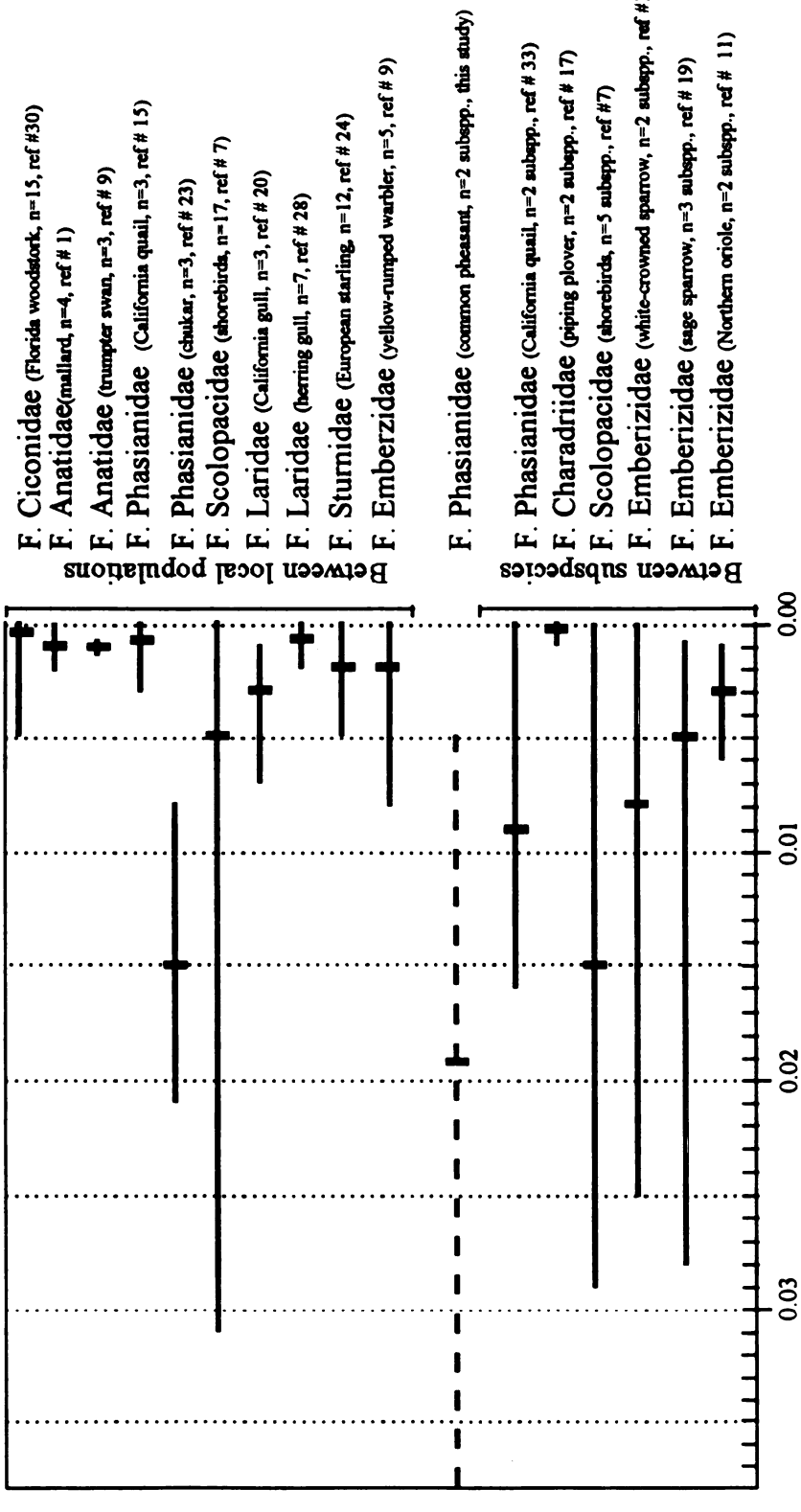

Figure 13. Means (●) and ranges (–) of observed genetic distances for members of the Class Aves between local populations of the same species (upper graph) and between subspecies (lower graph). Values are Nei (1978) unbiased genetic distances. Numbers in parentheses indicate number of populations or subspecies compared, and reference number from Appendix D.

Conclusions

Repeated releases over many years were often necessary before pheasants established self-maintaining populations within what is recognized as the range of common pheasants in North America (Prince et al. 1988). Releases of the Sichuan pheasant, *P. c. strauchi*, into Michigan habitats not traditionally used by ring-necked pheasants, *P. c. colchicus*, were made over a 10 year period beginning in 1986. Starch electrophoresis was used to examine levels of genetic heterogeneity and the introgression of Sichuan genes into existing ring-necked pheasant populations from 1991-1993. Results indicate Sichuan pheasants readily crossed with ring-necks as evidenced by the high rate of gene flow into the free-ranging populations. It is likely that several neighborhoods were sampled for each free-ranging population generating a Hardy-Weinberg disequilibrium condition that resulted in an excess in homozygotes, or Wahlund effect. Under such conditions, the expected average heterozygosity may be a more appropriate measure of genetic variation than the observed average heterozygosity.

Southern Michigan populations of pheasants currently show low levels of genetic heterogeneity. However, the expected average heterozygosity levels found in populations of pheasants from southern Michigan are similar to levels of other galliformes. This suggests that introduced pheasants in Michigan have experienced evolutionary forces similar to those of other populations of galliformes. The adaptation of genotypes to local environmental conditions is possible only if genetic heterogeneity exists. However, the persistence and maintenance of these levels will be dependent on the nature and extent of future evolutionary forces.

APPENDIX A

Electrophoretic Methodology and Techniques

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Sample Preparation

Liver tissue was homogenized 1-2 days prior to the electrophoretic run. Grinding procedures were as follows:

On the day prior to grinding:

prepare tissue grinding buffer (see below)
place ceramic mortars on ice and leave in ultra-cold freezer overnight

On the day of grinding:

place liver samples on ice
place tissue grinding buffer on ice
place 4 mg of liver tissue in grinding well (avoid adipose and connective tissue)
add 3-4 drops of tissue grinding buffer
homogenize tissue with pestle
place a 40 micron screen over homogenized tissue
place paper wicks on top of screen an allow them absorb the supernatant
place ELIZA trays on ice
fill each well of the ELIZA tray with one wick
double wrap the ELIZA tray with plastic
label and store ELIZA tray with wicks in the ultra cold freezer

Tissue Grinding Buffer

100 ml of 0.1 M Tris, pH 7.0

1.21 g Tris
50 ml distilled H_2O
adjust pH w/ 4M HCL
bring to volume with distilled H_20
store at 34 C

Starch Gels

6 mm horizontal gel

22 g potato starch
5 ml electrode buffer
195 ml distilled H_2O

10 mm horizontal gel

33 g potato starch
8 ml electrode buffer
292 ml distilled H_2O

heat above solution in a side arm flask over an open flame until boiling
deaerate solution, pour liquid gel solution into gel tray, remove any air bubbles
after gel has cooled, cover with plastic wrap to prevent desiccation
store at room temperature overnight
cool gel at 4 C for 1 hour prior to setting wicks

Electrode Buffer System and Running Conditions

Morpholine Citrate (Clayton and Tretiak, 1972)
ACON, AP, and IDH at pH 6.1
AP at pH 5.2

1 liter stock solution of Morpholine Citrate

8.4 g/l	citric acid, monohydrate
500 ml	distilled H_2O

store at 4 C overnight
pH with N-(3-amino propyl) morphline
bring to volume with distilled H_2O
store at 4 C

6 mm gels: run at 30 mAMPS (approx. 190 volts) for the first hour, 35-40 mAMPS (approx. 210 volts) for the remaining 5 hours

10 mm gels: run at 55 mAMPS (240 volts) for the first hour, 55-65 mAMPS(approx. 250 volts) for the remaining 5 hours

Histochemical Enzyme Specific Stains Used in This Study

ACON (Richardson et al. 1986)

100 ml	0.1 M Tris-HCl, pH 8.0
1 ml	cis-aconitic acid, pH 8.0
8 ml	1.0 M $MgCl_2$
25 mg	NADP
30 mg	MTT
2 mg	PMS
60 mg	isocitrate dehydrogenase

IDH (Richardson et al. 1986)

95 ml	0.1M Tris-HCl, pH 8.0
5 ml	0.1M $MgCl_2$
15 mg	NADP
15 mg	MTT
2 mg	PMS

ACP (Richardson et al. 1986)

100 ml	0.1M tris-HCl, pH 8.6
100 mg	β-napthyl acid phosphate
100 mg	Fast Blue RR salt
6 ml	0.1 M $MgCl_2$

AP (Richardson et al. 1986)

100 ml	0.05 M Na-acetate, pH 5.0
100 mg	α-napthyl acid phosphate
100 mg	Fast Garnet GBC salt

Stains were allowed to develop at room temperature in the dark. Staining time varied with enzyme, but ranged from 15 to 60 minutes.

Histochemical Enzyme Stain Buffers

0.1 M tris-HCl, pH 8.0 and 8.6

7.4 g	trisma base
6.1 g	trizma Hcl
100 ml	distilled H_2O

adjust pH w/ 1N HCl

0.05 M Na-acetate, pH 5.0

0.68 g	sodium acetate
100 ml	distilled H_2O

adjust pH with 1N HCl

cis-aconitic acid, pH 8.0

50 mg	cis-aconitic acid
100 ml	distilled H_2O

adjust pH w/ 4M NaOH

0.1 M $MgCl_2$

9.5 g	magnesium chloride
100 ml	distilled H_2O

Fixing Gels
Staining process was halted using 1% acetic acid
Gels were allowed to sit an fix in 50% ETOH for 1 hour
Gels were placed in ziplock bags for final storage

Chemical List (Sigma Chemical Co. 1995)

Sigma Order No.	Chemical Name(s)
A-6283	acetic acid, glacial
A-3412	cis-aconitic acid
A-9028	N-(3-amino propyl) morpholine
C-7129	citric acid, monohydrate
285-8	ethanol fixative (ETOH)
F-0500	Fast Blue RR salt
F-8761	Fast Garnet GBC salt, sulfate salt
H-7020	hydrochloric acid (HCl)
I-1877	isocitrate dehydrogenase
M-1028	magnesium chloride ($MgCl_2$)
M-2128	3-[4,5-dimethylthiazol-2-yl]-2,5-diaphenyletrazolium bromide, (MTT); thiazolyl blue
N-7000	α-napthyl acid phosphate, monosodium salt
N-7375	β-napthyl acid phosphate, monosodium salt
N-9511	β-nicotinamide adenine dinucleotide phosphate (NADP)
P-9625	phenazine methosulfate (PMS); N-methyldibenzopyrazine methyl suflate salt
S-8750	sodium acetate, anhydrous
S-5881	sodium hydroxide (NaOH)
T-1503	trizma base
T-3253	trizma-hydrochloride (tris-HCl)

Electrode Buffers used in the Screening Process

A. Morpholine-citrate (Clayton and Tretiak 1972)
pH 6.1 or 5.2
0.04 M citric acid - monohydrate
adjust pH using N-(3-aminopropyl) morpholine

Gel: 1:19 parts, electrode buffer to distilled H_20

B. Lithium-borate (Scandolis 1969)
pH 8.3
0.19 M boric acid
0.04M lithium hydroxide
adjust pH with dry ingredients

Gel: 1:10 parts, electrode buffer to 0.05 M tris - 0.007 M citric acid, pH 8.3

C. Tris-citrate (Meizel and Markert 1967)
pH 7.0
0.155 M tris
0.043 M citric acid - monohydrate
adjust pH with dry ingredients

Gel: 1:14 parts, electrode buffer to distilled H_2O

D. Tris-citrate (Shaw and Prasad 1970)

pH 8.0
0.687 tris
0.157 M citric acid - monohydrate
adjust pH with dry ingredients

Gel: 0.023 M tris , 0.001 M citric acid, monohydrate, distilled H_2O
pH with dry ingredients

E. Tris-versene-borate (Selander et al. 1971)

pH 8.0
0.5 M tris
0.5 M boric acid
0.016 M Na_2EDTA
adjust pH with dry ingredients

Gel: 1:10 parts, electrode buffer to distilled H_2O

F. Sodium borate (Poulik 1957)

pH 8.0
0.30 M boric acid
adjust pH with NaOH

Gel: 0.076 M tris, pH with citric acid

G. Phosphate (Richardson et al. 1986)

pH 7.0
11.6 mM Na_2HPO_4, anhydrous
8.4 mM NaH_2PO_4

Gel: 1:10 parts, electrode buffer to distilled H_2O

H. Phosphate-citrate (Shaw and Prasad 1970)

pH 8.0
0.214 M K_2HPO_4
0.027 M citric acid, monohydrate
pH with dry ingredients

Gel: 1.16 mM K_2HPO_4, 0.2 mM citric acid, monohydrate, distilled H_2O

I. Tris-maleate-EDTA-$MgCl_2$ (Richardson et al. 1986)

pH 7.8
0.05 M tris
1 mM NaEDTA
1 mM $MgCl_2$
20 mM maleic acid

Gel: 1:10 parts, electrode buffer to distilled H_2O

J. Sodium-borate (Ayala et al. 1972)

pH 8.65
0.3 M boric acid
0.06 M NaOH
Gel: 0.076 M tris, 0.005 M citric acid, distilled H_2O

K. Tris-borate (Shaw and Prasad 1970)

pH 7.5
0.0546 M tris
0.2354 boric acid

Gel: 0.198 mM tris, 5.5 mM boric acid

L. 0.5 M Phosphate (Shaw and Prasad 1970)

pH 7.0
87.0 g/l K_2HPO_4
68.0 g/l KH_2pO_4

Gel: 1:10 parts, electrode buffer to distilled H_2O

M. Tris-maleate (Richardson et al. 1986)

pH 7.8
50 mM trizma
20 mM maleic acid

Gel: 1:10 parts, electrode buffer to distilled H_2O

N. Tris-EDTA-borate-$MgCl_2$ (Richardson et al. 1986)

pH 7.8
0.015 M tris
0.005 M Na_2EDTA
0.01 M $MgCl_2$
0.05 M boric acid

Gel: 1:10 parts, electrode buffer to distilled H_2O

O. Citrate-phosphate (Richardson et al. 1986)

pH 6.4
2.5 mM citric acid
10 mM Na_2HPO_4

Gel: 1:10 parts, electrode buffer to distilled H_2O

Histochemical Stains used in the Screening Process

ACON - aconitase hydratase - E.C. # 4.2.1.3 (Richardson et al. 1986)

0.1 M tris-HCL , pH 8.0	100 ml
cis-aconitic acid, pH 8.0 (50 mg/ml)	1 ml
NADP	25 mg
$MgCl_2$	8 mg
MTT	30 mg
PMS	2 mg
isocitrate dehydrogenase	40 units

ALD - aldolase - E.C. # 4.1.2.13 (Wendel and Weeden 1989, Richardson et al. 1986)
also known as fructose-bisphosphate aldolase (FBA)

0.1 M tris-HCl, ph 7.4	100 ml
arsenate Na salt (6 mg/ml)	75 mg
fructose 1,6 diphosphate (Na_3)	200 mg
NAD	30 mg
MTT	30 mg
PMS	5 mg
glyceraldehyde-3-phosphate dehydrogenase	100 units
triose phosphate isomerase	100 units

ADH - alcohol dehydrogenase - E.C. # 1.1.1.1 (Shaw and Prasad 1970, Richardson et al. 1986)

0.1 M tris-HCl, pH 8.0	89 ml
ethanol (95%)	6 ml
0.1 M NaCN	5 ml
PMS	4 mg
MTT	20 mg
NAD	20 mg

AP - alkaline phosphatase - E.C. # 3.1.3.1 (Ayala et al. 1972, Shaw and Prasad 1970, Richardson et al. 1986)

0.1 M tris-HCl, pH 8.6	100 ml
Fast Blue RR or Fast Blue BB salts	100 mg
β-napthyl acid phosphate	100 mg
$MgCl_2$	60 mg
$MnCl_2$	60 mg

AK - adenylate kinase - E.C. # 2.7.4.3 (Wendel and Weeden, 1989, Ayala et al. 1972, Richardson et al. 1986)

0.1 M tris-HCL, pH 8.0	100 ml
glucose	90 mg
$MgCl_2$	20 mg
NADP	30 mg
ADP	40 mg
PMS	4 mg
MTT	30 mg
glucose-6-phosphate dehydrogenase	80 units

ACP - acid phosphatase - E.C. # 3.1.3.2 (Richardson et al. 1986)

0.05 M Na-acetate, pH 5.0	100 ml
α-Na-napthyl acid phosphate	100 mg
Fast Garnet GBC salt	100 mg
$MgCl_2$	10 mg

AAT- aspartate aminotransferase - E.C. # 2.6.1.1 (O'Malley et al. 1980, Richardson et al. 1986)
Also known as glutamic oxaloacetate transaminase (GOT)

0.1 M tris-HCl, pH 8.0	100 ml
L-aspartic acid	200 mg
Fast Blue BB, Fast Garnet GBC, or Fast Violet B salt	150 mg

CK - creatine kinase - E.C. # 2.7.3.2 (Shaw and Prasad 1970, Richardson et al. 1986)

0.1 M tris-HCl, pH 8.0	100 ml
creatine phosphate	731 mg
glucose	90 mg
ADP	75 mg
$MgCl_2$	21 mg
NADP	25 mg
MTT	20 mg
PMS	5 mg
hexokinase	160 units
glucose-6-phosphate dehydrogenase	80 units

EST- esterase - E.C. # 3.1.1.1 (Wendel and Weeden 1989, Richardson et al. 1986)

0.1 M tris-maleate, pH 6.5	100 ml
α or β-napthyl acetate (in 2 ml acetone)	50 mg
Fast Blue RR salt or Fast Garnet GBC salt	100 mg

FDP - fructose 1.6 diphosphate - E.C. # 3.1.3.11 (O'Malley et al. 1980, Wendel and Weeden 1989, Richardson et al. 1986)
also known as fructose-bisphosphatase (FBP)

0.1 M tris-HCl, pH 8.0	100 ml
$MgCl_2$	100 mg
NADP	20 mg
MTT	20 mg
PMS	20 mg
fructose 1.6 diphosphate	120 units
phosphoglucose isomerase	80 units
glucose-6-phosphate dehydrogenase	80 units

FUM- fumarase hydratase - E.C. # 4.2.1.2 (Wendel and Weeden 1989, Richardson et al. 1986)

0.1 M tris-HCl, pH 8.0	100 ml
NAD	20 mg
MTT	20 mg
PMS	2 mg
fumaric acid, Na salt	200 mg
malate dehydrogenase	200 units

GDH - glutamate dehydrogenase - E.C. # 1.4.1.3 (Wendel and Weeden 1989, Richardson et al. 1986)

0.1 M tris-HCl, pH 8.0	80 ml
glutamate (glutamic acid)	100 mg
NAD	20 mg
MTT	10 mg
PMS	2 mg

αGPDH - α-glycerol-3-phosphate dehydrogenase - E.C. # 1.1.1.8 (Shaw and Prasad 1970, Richardson et al. 1986)

0.1 M tris-HCl, pH 7.0	100 ml
0.1 M NaCN	10 ml
1 M Na-α-glycerophosphate, pH 7.0	10 ml
NAD	50 mg
MTT	30 mg
PMS	2 mg

G3PDH - glyceraldehyde-3-phosphate dehydrogenase - E.C. # 1.2.1.12 (Ayalya et al. 1972, Richardson et al. 1986)

also known as triosephosphate dehydrogenase

0.1 M tris-HCl, pH 8.0	100 ml
NAD	50 mg
MTT	30 mg
PMS	4 mg
arsenic acid, Na salt	150 mg
aldolase	100 units
glyceraldehyde-3-phosphate	200 units

G6PDH - glucose-6-phosphate dehydrogenase - E.C. # 1.1.1.49 (Richardson et al. 1986)

0.1 M tris-HCl, pH 8.0	100 ml
NADP	20 mg
$MgCl_2$	20 mg
MTT	20 mg
PMS	5 mg
D-glucose-6-phosphate	200 units

HEX - hexokinase - E.C. # 2.7.1.1 (Richardson et al. 1986)

0.1 M tris-HCl, pH 8.6	100 ml
NADP	20 mg
$MgCl_2$	20 mg
MTT	20 mg
PMS	2 mg
ATP	6 mg
D-glucose	20 mg
glucose-6-phosphate dehydrogenase	10 units

IDH - isocitrate dehydrogenase - E.C. # 1.1.1.42 (Wendel and Weeden 1989, Richardson et al. 1986)

0.1 M tris-HCl, pH 8.0	100 ml
isocitric acid (Na_3)	100 mg
$MgCl_2$	5 mg
NADP	15 mg
MTT	15 mg
PMS	2 mg

LDH - lactate dehydrogenase - E.C. # 1.1.1.27 (Selander et al. 1971, Richardson et al. 1986)

0.1 M tris-HCl, pH 8.0	100 ml
0.5 M lithium DL lactate	800 mg
NAD	40 mg
MTT	8 mg
PMS	16 mg

MDH - malate dehydrogenase - E.C. 1.1.1.37 (Richardson et al. 1986)

0.1 M tris-HCl, pH 8.0	50 ml
0.2 M Na-malate buffer, pH 8.0	50 ml
NAD	30 mg
MTT	20 mg
PMS	5 mg

0.2 M Na-malate buffer

DL- malic acid	26.88g/l
NaOH	16 g/l

adjust pH with 2 N NaOH

MPI - mannose phosphate isomerase - E.C. # 5.3.1.8 (Nichols and Ruddle 1973, Richardson et al. 1986)

0.1 M tris-HCl, pH 8.0	100 ml
mannose-6-phosphate	34 mg
NADP	35 mg
MTT	35 mg
PMS	7 mg
$MgCl_2$	40 mg
glucose-6-phosphate isomerase	100 units
glucose-6-phosphate dehydrogenase	100 units

ME - malic enzyme - E.C. # 1.1.1.40 (Ayala et al. 1972, Richardson et al. 1986)

0.1 M tris-HCl, pH 7.4	100 ml
$MgCl_2$	25 mg
NADP	25 mg
MTT	20 mg
PMS	5 mg
malic acid	50 mg

PGI - phosphoglucoisomerase - E.C. 5.3.1.9 (Selander et al. 1971, Richardson et al. 1986)

also known as glucose-6-phosphate isomerase (GPI)

0.1 M tris-HCl, pH 8.0	100 ml
$MgCl_2$	20 mg
NADP	20 mg
MTT	20 mg
PMS	4 mg
disodium fructose-6-phosphate	50 mg
glucose-6-phosphate dehydrogenase	20 units

PGM - phosphoglucomutase - E.C. # 2.7.5.1 (Wendel and Weeden 1989, Richardson et al.1986)

0.1 M tris-HCl, pH 8.0	100 ml
$MgCl_2$	10 mg
NADP	10 mg
MTT	10 mg
PMS	2 mg
glucose-1-phosphate, Na_2 salt	50 mg
glucose-6-phosphate dehydrogenase	40 units

6PGD - phophoglucconate dehydrogenase - E.C. # 1.1.1.44 (Wendel and Weeden 1989, Richardson et al. 1986)

0.1 M tris-HCl, pH 8.0	100 ml
$MgCl_2$	10 mg
NADP	10 mg
MTT	10 mg
PMS	5 mg
6-phophogluconic acid (Na or Ba salt)	20 mg

PEP - peptidase - E.C. # 3.4.11 (Richardson et al. 1986)

0.1 M tris-HCl, pH 8.0	100 ml
peroxidase	20 mg
o-dianisidine (di-HCL salt)	10 mg
peptide (see below)	10 mg
L-amino acid oxidase (snake venom)	10 mg
$MgCl_2$	20 mg

PEP - A = valine-leucine
PEP - B = leucine-glucine-glucine
PEP - C = lysine-leucine
PEP - D = phenylalanine-proline

SDH - sorbitol dehydrogenase - E.C. 1.1.1.14 (Shaw and Prasad 1970, Richardson et al. 1986)
also known as L-iditol dehydrogenase (SORH)

0.1 M tris-HCl, pH 8.0	100 ml
sorbitol	500 mg
NAD	10 mg
MTT	15 mg
PMS	2 mg

SOD - superoxide dismutase - E.C. # 1.15.1.1 (Wendel and Weeden 1989, Richardson et al. 1986)

0.1 M tris-HCl, pH 8.0	100 ml
riboflavin	4 mg
EDTA	2 mg
MTT	20 mg
PMS	5 mg

TPI - triose phosphate isomerase - E.C. # 5.3.1.1 (Richardson et al. 1986)

0.1 M tris-HCl, pH 8.0	100 ml
DL-α-glycerophosphate (DHAP)	2 g
pyruvic acid	1.1 g
NAD	50 mg
MTT	30 mg
PMS	5 mg
arsenate	50 mg
glycerophosphate dehydrogenase	200 units
lactate dehydrogenase	200 units

XDH - xanthine dehydrogenase - E.C. # 1.1.1.204 (Richardson et al. 1986)

0.1 M tris-HCl, pH 8.0	100 ml
hypoxanthine	50 mg
NAD	20 mg
MTT	20 mg
PMS	10 mg

APPENDIX B

Allele Frequencies by Year

APPENDIX B

Allele Frequencies by Year

Allele frequencies of common pheasants in southern Michigan harvested in Montcalm and Hillsdale counties during 1991.

Locus	Allele	Montcalm	Hillsdale
ACP	1	0.80	0.88
	2	0.20	0.12
	n	15	20
AP	1	0.71	0.90
	2	0.29	0.10
	n	12	20
IDH-1	1	0.46	0.98
	2	0.54	0.02
	n	14	20
IDH-2	1	1.00	1.00
	2	0.00	0.00
	n	14	20
ACON-1	1	0.14	0.28
	2	0.86	0.72
	n	14	20
ACON-2	1	0.04	0.00
	2	0.96	1.00
	n	14	20

Allele frequencies, by year for 3 populations of free-ranging common pheasants harvested in southern Michigan.

Locus	Allele	free-ranging								
		w/o releases			w/releases					
		ring-necked			mixed			Sichuan		
		1991	1992	1993	1991	1992	1993	1991	1992	1993
ACP	1	0.84	1.00	0.50	0.92	0.89	0.88	0.84	1.00	1.00
	2	0.16	0.00	0.50	0.08	0.11	0.12	0.16	0.00	0.00
	n	35	8	6	20	33	7	32	3	10
AP	1	0.83	0.50	0.83	0.72	0.44	0.31	0.86	0.88	0.85
	2	0.17	0.50	0.17	0.28	0.56	0.69	0.14	0.12	0.15
	n	32	8	6	20	32	7	32	3	10
IDH-1	1	0.77	0.81	0.58	0.55	0.80	0.32	0.89	1.00	0.95
	2	0.23	0.19	0.42	0.45	0.20	0.38	0.11	0.00	0.05
	n	34	8	5	20	32	7	32	3	10
IDH-1	1	1.00	1.00	1.00	0.55	1.00	1.00	1.00	1.00	1.0
	2	0.00	0.00	0.00	0.45	0.00	0.00	0.00	0.00	0.0
	n	34	8	6	20	33	7	32	3	10
ACON1	1	0.22	0.12	0.67	0.60	0.32	0.06	0.36	0.25	0.30
	2	0.78	0.88	0.33	0.40	0.682	0.94	0.64	0.75	0.70
	n	34	8	6	21	33	7	32	3	10
ACON2	1	0.02	0.44	0.30	1.00	0.77	1.00	1.00	0.88	1.00
	2	0.98	0.56	0.70	0.00	0.23	0.00	0.00	0.12	0.00
	n	34	8	6	22	33	7	32	3	10

APPENDIX C

Genetic Heterogeneity in the Class Aves

Genetic variability of various avian species found in North America.

Taxonomic Classification			Common Name	Scientific Name	# indivs.	# pops	# loci	H_{obs}	H_{exp}	Reference
O. Ciconiiformes	F. Ardeidae		great-blue heron	*Areda herodias*	46	2	46	0.070	-	18
	F. Ciconiidae		Florida woodstork	*Mycteria americana*	396	15	16	0.093	-	35
O. Anseriformes	F. Anatidae		trumpter swan	*Olor buccinator*	194	3	13	0.010	-	8
			brant	*Branta bernicla*	94	3	28	0.030	-	27
			American black duck	*Anas rubripes*	131	3	29	0.053	-	1
			mallard	*Anas platyrhynchos*	181	4	29	0.059	-	1
			American wigeon	*Anas americana*	629	17[1]	25	0.084	-	29
O. Galliformes	F. Phasianidae	SF. Phasianinae	ring-necked pheasant	*Phasianus colchicus*	13	1	27	0.026	-	17
			ring-necked pheasant	*Phasianus colchicus*	177	7	41	0.027	0.034	37
			ring-necked pheasant	*Phasianus colchicus*	192	4	6	0.023	0.049	*
			ring-necked pheasant	*P. c. torquatus*	10	?	26	0.049	-	32
			Bianchi's pheasant	*P. c. bianchi*	10	?	26	0.038	-	32
			S. Caucasian pheasant	*P. c. colchicus*	10	?	26	0.066	-	32
			chukar	*Alectoris chukar*	12	1	27	0.052	-	17
			chukar	*Alectoris chukar*	45	3	33	0.061	0.063	28
			lesser prairie chicken	*Tympanuchus pallidicinctus*	13	1	27	0.000	-	17
			willow ptarmigan	*Lagopus lagopus*	269	6	23	0.082	-	20
			willow ptarmigan	*L. lagopus*	640	5	23	0.083	-	19
			rock ptarmigan	*L. mutus*	45	6	23	0.044	-	20

[1] number of sampling periods * this study

Genetic variability of various avian speices found in North America cont.

Taxonomic Classification			Common Name	Scientific Name	# indivs.	# pops	# loci	H_{obs}	H_{exp}	Reference
O. Galliformes	F. Phasianidae	SF. Odotophorinae	California quail	*Lophortyx californicus*	36	3	27	0.026	-	17
			California quail	*L. californicus*	101	7	37	0.032	0.038	41
			Gambel's quail	*L. gambelii*	22	1	27	0.025	-	17
			scaled quail	*Callipepla squarnata*	29	2	27	0.026	-	17
			Northern bobwhite	*Colinus virginianus*	15	2	27	0.027	-	17
			mountain quail	*Oreortyx pictus*	16	1	27	0.021	-	17
			Montezuma quail	*Cyrtonyx montesumae*	31	2	27	0.038	-	17
O. Gruiformes	F. Rallidae		king rail	*Rallus elegans*	10	?	38	0.040	-	6
			clapper rail	*R. longirostris*	7	?	38	0.030	-	6
O. Charadriiformes	F. Charadriidae		lesser golden plover	*Pluvialis dominica*	10	?	40	-	0.021	7
			black-bellied plover	*P. squatarola*	13	?	40	-	0.011	7
			killdeer	*Charadrius vocifercus*	12	?	40	-	0.004	7
			Wilson's plover	*C. wilsonia*	7	?	40	-	0.009	7
			snowy plover	*C. alexandrius*	7	?	40	-	0.011	7
			mountain plover	*C. montanus*	10	?	40	-	0.000	7
			semipalmated plover	*C. semipamatus*	15	?	40	-	0.000	7
			piping plover - Atlantic	*C. melodus melodus*	16	1	36	0.003	0.011	22
			piping plover - Inland	*C. m. circuncinctus*	106	4	36	0.020	0.020	22
O. Charadriiformes	F. Scolopacidae	Tribe Tringini	terek sandpiper	*Xenus cinereus*	13	?	29-40	-	0.019	7
			willet	*Catoptrophorus*	23	2	29-40	-	0.002	7

Genetic variability of various avian species found in North America cont.

Taxonomic Classification			Common Name	Scientific Name	# indivs.	# pops	# loci	H_{obs}	H_{exp}	Reference
O. Charadriiformes	F. Charadriidae	Tribe Limsoini	Hudsonian godwit	*Limosa haemastica*	31	?	29-40	-	0.021	7
		Tribe Calidridini	redknot	*Calidris canutus*	40	4	29-40	-	0.035	7
			purple sandpiper	*C. maritima*	35	2	29-40	-	0.006	7
			least sandpiper	*C. minutilla*	25	3	29-40	-	0.030	7
			white-rumped sandpiper	*C. fuscicollis*	56	2	29-40	-	0.023	7
			dunlin	*C. alpina*	25	3	29-40	-	0.009	7
			Western sandpiper	*C. mauri*	31	2	29-40	-	0.019	7
			rufous stint	*C. ruficollis*	30	?	29-40	-	0.028	7
			curlew sandpiper	*C. ferruginea*	28	?	29-40	-	0.037	7
			semipalmated sandpiper	*C. pusilla*	25	?	29-40	-	0.038	7
		Tribe Limnodromini	long-billed dowitcher	*Limnodromus scolopaceus*	8	?	36	0.050	-	6
			short-billed dowitcher	*L. griseus*	6	?	36	0.020	-	6
			short-billed dowitcher	*L. griseus*	23	2	29-40	-	0.016	7
O Charadriiformes	F. Laridae	SF. Larinae	California gull	*Larus californicus*	23	15	32	0.031	0.028	25
			herring gull	*L. argentatus*	80	15	34	0.023	-	34
			lesser black-backed gull	*L. fuscuc*	80	15	34	0.009	-	34
			Iceland gull	*L. glaucoides*	80	15	34	0.029	-	34
			glaucous gull	*L. hyperboreus*	80	15	34	0.044	-	34
			greater black-backed gull	*L. marinus*	80	15	34	0.006	-	34
		SF. Sterninae	Forester's tern	*Sterna Forsteri*	25	3	23	0.038	-	21

Genetic variability of various avian species found in North America cont.

Taxonomic Classification		Common Name	Scientific Name	# indivs.	# pops	# loci	H_{obs}	H_{exp}	Reference
O. Piciformes	F. Picidae	red-shafted flicker	*Colaptes auratus auratus*	5	?	?	0.100	-	16
		yellow-shafted flicker	*C. suratus cafer*	7	?	?	0.083	-	16
		William's sapsucker	*Sphyrapicus thyroides*	18	1	39	0.016	0.015	24
		yellow-bellied sapsucker	*S. varius*	7	1	39	0.045	0.046	24
		red-naped sapsucker	*S. nuchalis*	34	3	39	0.043	0.048	24
		red-breasted sapsucker	*S. ruber*	13	1	39	0.022	0.032	24
		red-cockaded woodpecker	*Picoides borealis*	442	26	16	-	0.078	36
O. Passeriformes	F. Tyrannidae	willow flycatcher	*Empidonax traill*	65	4	36	0.074	0.079	32
		willow flycatcher	*E. traill*	20	1	38	0.069	0.088	39
		alder flycatcher	*E. alnorum*	29	2	36	0.076	0.083	32
		alder flycatcher	*E. alnorum*	17	1	38	0.071	0.079	39
		yellow-bellied flycatcher	*E. flaviventris*	19	1	38	0.059	0.081	39
		acadian flycatcher	*E. virescens*	10	1	38	0.087	0.091	39
		least flycatcher	*E. minimus*	22	1	38	0.050	0.054	39
		Hammond's flycatcher	*E. hammondii*	13	1	38	0.053	0.060	39
		gray flycatcher	*E. wrightii*	18	1	38	0.047	0.047	39
		dusky flycatcher	*E. oberholseri*	17	4	38	0.063	0.073	39
		Western flycatcher	*E. difficilis*	16	1	38	0.049	0.050	39
		olive-sided flycatcher	*Contopus borealis*	8	1	38	0.038	0.043	39
		Western wood-pewee	*C. sordidulus*	5	1	38	0.067	0.079	39
		Eastern wood-pewee	*C. virens*	7	1	38	0.084	0.096	39

Genetic variability of various avian species found in North America cont.

Taxonomic Classification			Common Name	Scientific Name	# indivs.	# pops	# loci	H_{obs}	H_{exp}	Reference
O. Passeriformes	F. Paridae		tufted titmouse	*Parus bicolor bicolor*	3	?	36	0.060	-	6
			tufted titmouse	*P. bicolor bicolor*	75	1	36	0.060	-	11
			black-crested titmouse	*P. b. atricristatus*	5	?	36	0.060	-	6
			black-crested titmouse	*P. b. atricristatus*	75	1	36	0.060	-	11
O. Passeriformes	F. Muscicapidae	SF. Sylviinae	ruby-crowned kinglet	*Regulus calendula*	10	?	?	0.048	0.040	2
		SF. Turdinae	wood thrush	*Hylocichla mustelina*	5	?	25-27	0.104	0.065	2
			veery	*Catharus fuscescens*	5	?	25-27	0.056	0.052	2
			hermit thrush	*C. guttatus*	13	?	25-27	0.048	0.047	2
			grey-cheeked thrush	*C. minimus*	2	?	25-27	0.021	0.016	2
			Swainson's thrush	*C. ustulatus*	17	?	25-27	0.053	0.052	2
			Swainson's thrush	*C. ustulatus*	5	?	26	0.032	-	4
			American robin	*Turdis migratorius*	10	?	25-27	0.042	0.033	2
			Eastern bluebird	*Sialia sialia*	7	?	25-27	0.048	0.040	2
O. Passeriformes	F. Mimidae		gray catbird	*Dumetella carolinensis*	8	?	25-27	0.034	0.030	2
			gray catbird	*D. carolinensis*	24	?	23	0.018	-	5
			Northern mockingbird	*Mimus polyglottos*	8	?	23	0.010	-	5
			brown thrasher	*Toxostoma rufum*	7	?	23	0.048	-	5
			curve-billed thrasher	*T. curvirostre*	4	?	23	0.000	-	5
			crissal thrasher	*T. dorsale*	1	?	23	0.000	-	5

Genetic variability of various avian species found in North America cont.

Taxonomic Classification			Common Name	Scientific Name	# indivs.	# pops	# loci	H_{obs}	H_{exp}	Reference
O. Passeriformes	F. Sturnidae		European starling	*Sturnus vulgaris*	597	12	24	0.034	0.038	30
O. Passeriformes	F. Vireonidae		white-eyed vireo	*Vireo griseus*	5	?	23	0.036	-	5
			Philadelphia vireo	*V. philadelphicus*	1	?	23	0.000	-	5
			yellow-throated vireo	*V. flavifrons*	4	?	23	0.043	-	5
			solitary vireo	*V. solitarius*	16	?	23	0.054	-	5
			red-eyed vireo	*V. olivaceus*	58	?	23	0.048	-	5
			red-eyed vireo	*V. olivaceus*	5	?	26	0.022	-	4
O. Passeriformes	F. Emberizidae	SF. Parulinae	black-and-white warbler	*Mniotilta varia*	6	?	18-24	0.026	-	4
			black-and-white warbler	*M. varia*	8	?	17	-	0.092	10
			golden-winged warbler	*Vermivora chrysoptera*	2	?	18-24	0.048	-	4
			goldern-winged warbler	*V. chrysoptera*	40	2	40	0.065	0.071	15
			blue-winged warbler	*V. pinus*	1	?	18-24	0.095	-	4
			blue-winged warbler	*V. pinus*	20	?	40	0.052	0.058	15
			Tennessee warbler	*V. peregrina*	24	?	18-24	0.065	-	4
			Tennessee warbler	*V. peregrina*	13	?	21	-	0.226	10
			orange-crowned warbler	*V. celata*	12	?	18-24	0.040	-	4
			orange-crowned warbler	*V. celata*	8	?	21	-	0.221	10
			Nashville warbler	*V. ruficapilla*	22	?	22	0.042	0.123	10
			Northern parula	*Parula americana*	6	?	18-24	0.030	-	4
			Northern parula	*P. americana*	2	?	15	-	0.100	10
			yellow warbler	*Dendroica petechia*	2	?	18-24	0.068	-	4

Genetic variability of various avian species found in North America cont.

Taxonomic Classification			Common Name	Scientific Name	# indivs.	# pops	# loci	H_{obs}	H_{exp}	Reference
O. Passeriformes	F. Emberizidae	SF. Parulinae cont.	chestnut-sided warbler	*Dendroica pensylvanica*	10	?	18-24	0.014	-	4
			black-throated warbler	*D. caerulescens*	6	?	18-24	0.040	-	4
			pine warbler	*D. pinus*	2	?	18-24	0.050	-	4
			black-throated green warbler	*D. virens*	2	?	18-24	0.024	-	4
			prairie warbler	*D. discolor*	8	?	18-24	0.012	-	4
			cape-may warbler	*D. tigrina*	6	?	18-24	0.033	-	4
			blackburnian warbler	*D. fusca*	8	?	18-24	0.036	-	4
			magnolia warbler	*D. magnolia*	12	?	18-24	0.004	-	4
			magnolia warbler	*D. magnolia*	14	?	22	-	0.137	10
			yellow-rumped warbler	*D. coronata*	10	?	18-24	0.005	-	4
			yellow-rumped warbler	*D. coronata*	21	3	32	0.031	0.037	9
			yellow-rumped warbler	*D. coronata*	21	2	32	0.031	0.037	9
			yellow-rumped warbler	*D. coronata*	35	?	22	0.039	0.121	10
			palm warbler	*D. palmarum*	33	?	18-24	0.031	-	4
			palm warbler	*D. palmarum*	12	?	22	0.047	0.134	10
			bay-breasted warbler	*D. castanea*	12	?	18-24	0.024	-	4
			black-poll warbler	*D. striata*	6	?	22	-	0.023	10
			American redstart	*Setophaga ruticilla*	16	?	18-24	0.031	-	4
			American redstart	*S. ruticills*	12	?	20	-	0.253	10

Genetic variability of various avaian species found in North America cont.

Taxonomic Classification			Common Name	Scientific Name	# indivs.	# pops	# loci	H_{obs}	H_{exp}	Reference
O. Passeriformes	F. Emberizidae	SF. Parulinae cont.	ovenbird	*Seiurus aurocapillus*	29	?	18-24	0.061	-	4
			ovenbird	*S. aurocapillus*	10	?	22	-	0.177	10
			Northern waterthrush	*S. noveboracensis*	7	?	18-24	0.128	-	4
			Northern waterthrush	*S. noveboracensis*	24	?	22	-	0.222	10
			Swainson's warbler	*Limnothlypis swainsonii*	2	?	18-24	0.100	-	4
			worm-eating warbler	*Helmitheros vermivorous*	2	?	18-24	0.055	-	4
			prothonotary warbler	*Protonotaria citrea*	2	?	18-24	0.050	-	4
			common yellowthroat	*Geothylpis trichas*	32	?	18-24	0.037	-	4
			common yellowthroat	*G. trichas*	16	?	21	-	0.123	10
			common yellowthroat	*G. trichas*	27	4	30	0.070	-	40
			Kentucky warbler	*G. formosa*	16	?	18-24	0.056	-	4
			hooded warbler	*Wilsonia citrina*	6	?	18-24	0.015	-	4
			Canada warbler	*W. canadensis*	2	?	16	-	0.438	10
			yellow-breasted chat	*Icteria virens*	5	?	18-24	0.020	-	4
			morning warbler	*Oporonis philodelphia*	8	?	18	-	0.117	10
O. Passeriformes	F. Emberizidae	SF. Emberizinae	song sparrow	*Melospiza melodia*	7	?	20-22	0.019	-	3
			song sparrow	*M. melodia*	14	3	39	0.042	-	38
			swamp sparrow	*M. georgiana*	10	?	20-22	0.051	-	3
			swamp sparrow	*M. georgiana*	16	2	39	0.042	-	38

Genetic variability of various avain species found in North America cont.

Taxonomic Classification			Common Name	Scientific Name	# indivs.	# pops	# loci	H_{obs}	H_{exp}	Reference
O. Passeriformes	F. Emberizidae	SF. Emberizinae	Lincon's sparrow	*Melospiza lincolnii*	8	3	39	0.054	-	38
			white-throated sparrow	*Zonotrichia albicollis*	10	?	20-22	0.079	-	3
			white-throated sparrow	*Z. albicollis*	12	3	39	0.032	-	38
			white-crowned sparrow	*Z. leucophrys*	121	8	46	0.056	0.099	13
			white-crowned sparrow	*Z. leucophrys*	19	2	19	0.036	-	38
			white-crowned sparrow	*Z. l. nuttalli*	89	5	44	0.054	-	12
			white-crowned sparrow	*Z. l. pugetensis*	36	2	44	0.061	-	12
			rufous-collared sparrow	*Z. capensis*	20	14	20	0.031	0.036	26
			golden-crowned sparrow	*Z. atricapilla*	15	1	39	0.039	-	38
			Harris' sparrow	*Z. querula*	18	2	39	0.020	-	38
			dark-eyed junco	*Junco hyemalis*	10	?	20-22	0.058	-	3
			dark-eyed junco	*J. hyemalis*	48	2	39	0.029	-	38
			savannah sparrow	*Ammodramus sandwichensis*	10	?	20-22	0.049	-	3
			Henslow's sparrow	*A. henslowii*	3	?	20-22	0.076	-	3
			grasshopper sparrow	*A. savannarum*	10	?	20-22	0.045	-	3
			fox sparrow	*Passerella iliaca*	57	3	39	0.036	-	38
			chipping sparrow	*Spizella passerina*	11	?	20-22	0.065	-	3
			field sparrow	*S. pusilla*	6	?	20-22	0.083	-	3
			brown towhee	*Pipilo fuscus*	5	?	20-22	0.010	-	3
			green-tailed towhee	*P. chlorurus*	2	1	39	0.058	-	38
			sage sparrow - coastal	*Amphispiza belli belli*	118	8	41	0.037	-	23

Genetic variability of various avian species found in North America cont.

Taxonomic Classification	Common Name	Scientific Name	# indivs.	# pops	# loci	H_{obs}	H_{exp}	Reference
O. Passeriformes F. Emberizidae SF. Emberizinae cont.	sage sparrow - continental	*Amphispiza belli nevadensis*	154	9	41	0.047	-	23
	sage sparrow - mohave	*A. b. canescens*	85	5	41	0.040	-	23
	black-throated sparrow	*A. bilineata*	7	?	20-22	0.072	-	3
	chestnut-collared longspur	*Calcarius ornatus*	3	?	20-22	0.061	-	3
O. Passeriformes F. Emberizidae SF. Icterinae	boat-tailed grackle	*Quiscalus major*	8	?	38	0.001	-	6
	boat-tailed grackle	*Q. major*	?	?	15	-	0.179	33
	great-tailed grackle	*Q. mexicanus*	6	?	30	0.001	-	6
	common grackle	*Q. quiscula*	?	?	15	-	0.164	33
	brown-headed cowbird	*Molothrus ater*	?	?	15	-	0.181	33
	red-winged blackbird	*Agelaius phoeniceus*	?	?	15	-	0.218	33
	Eastern meadowlark	*Sturnella magna*	?	?	15	-	0.210	33
	Western meadowlark	*S. neglecta*	?	?	15	-	0.186	33
	Brewers' blackbird	*Euphagus cyanocephalus*	?	?	15	-	0.086	33
	Northern oriole	*Icterus galbula*	432	8	?	0.056	-	14
O. Passeriformes F. Frigillidae	purple finch	*Carpodacus purpureus*	4	?	15	0.036	-	3

References: 1. Ankney et al. (1986), 2. Avise et al. (1980a), 3. Avise et al. (1980b), 4. Avise et al. (1980c), 5.Avise et al. (1982), 6. Avise and Zink (1988), 7. Baker and Strauch (1988), 8. Barrett and Vyse (1982), 9. Barrowclough (1980b), 10. Barrwoclough and Corbin (1978), 11.Braun et al. (1984), 12. Corbin (1981), 13. Corbin and Wilkie (1988), 14. Corbin et al. (1979), 15. Gill (1987), 16. Grudzien and Moore (1986), 17. Gutierrez et al. (1983), 18. Gutman et al. (1980), 19. Gyllensten (1985), 20. Gyllensten et al. (1979), 21. Hackett (1989), 22. Haig and Oring (1988), 23. Johnson and Martin (1992), 24. Johnson and Zink (1983), 25. Karl et al. (1987), 26. Lougheed and Handford (1992), 27. Novak et al. (1989), 28. Randi et al. (1992), 29. Rhodes et al. (1993), 30. Ross (1983), 31. Scribner et al. (1989), 32. Seutin and Simon (1988), 33. Smith and Zimmerman (1976), 34. Snell (1991), 35. Stangel et al. (1990), 36. Stangel et al. (1992), 37. Warner et al. (1988), 38. Zink (1982), 39. Zink and Johnson (1984), 40. Zink and Klicka (1990), 41. Zink et al. (1987).

APPENDIX D

Genetic Distances and F_{ST} Values in the Class Aves

Literature values of Nei's (1978) genetic distance (D) and Wright's F_{ST} values for various avian species found in North America.

Taxonomic Classification	D w/in subfamily		D w/in genera			D between subspp. or between local[a] populations			F_{ST}	Ref[b]
	mean	range	Genus	mean	range	species	mean	range		
O. Ciconiiformes F. Ciconiae SF. Ciconiidae	-	-	*Mycteria*	-	-	*M. americana* Florida woodstork	0.0004[c]	0.000-0.005	0.019	30
O. Anseriformes F. Anatidae SF. Anserinae	-	-	*Branta*	-	-	*B. bernicla* Brant	-	-	0.013	22
	-	-	*Olor*	-	-	*O. buccinator* tundra swan	0.001[c]	0.001 - 0.001	-	8
	-	-	*Anas*	0.0006	0.000-0.002	*A. platyrhynchos* mallard	0.001	0.000-0.002	-	1
O. Galliformes F. Phasianidae SF. Phasianinae	0.425	0.003-0.993	*Alectoris*	0.208	0.003-0.312	*A. chukar* chukar	0.015	0.008-0.021	0.09	23
	-	-	*Phasianus*	-	-	*P. colchicus* ring-necked pheasant	0.055	-	0.022	26
SF. Odontophorinae	0.412	0.082-0.746	*Lophortyx*	0.007	0.005-0.008	*L. californicus* California quail	0.0007[c]	-0.015-0.003	0.007	15
	-	-	*Lophortyx*	-	-	*L. californicus* California quail	0.009	0.000-0.016	0.032	33
O. Gruiformes F. Rallidae SF. Rallinae	-	-	*Rallus* rails	0.004	-	-	-	-	-	6
O. Charadriiformes F. Charadriidae SF. Charadriinae	-	-	*Charadrius*	-	-	*C. melodus* piping plover	0.0015	0.000-0.008	0.022	17

Literature values of Nei's (1978) genetic distance (D) and Wright's F_{ST} values for various avian species found in North America cont.

Taxonomic Classification	D w/in subfamily		D w/in genera			D between subspp. or between local* populations			F_{ST}	Ref[1]
	mean	range	Genus	mean	range	species	mean	range		
O. Charadriiformes										
F. Scolopacidae	0.628	0.218-0.994	Charadrius	0.138	0.000-0.039	*C. cantus*	0.015	0.000-0.028	0.033	7
SF. Scolopacinae						red knot				
	-	-	*Limnodromus*	0.060	-	-	-	-		6
			dowitchers							
F. Laridae	-	-	*Larus*	-	-	*L. californicus*	0.003*	0.001-0.007	0.067	20
SF. Larinae						California gull				
	-	-	*Larus*	0.0021	0.000-0.009	*L. argentatus*	0.0006*	0.000-0.002	0.108	28
						herring gull				
SF. Sterninae	-	-	*Sterna*	0.170	0.000-0.510	-	-	-	-	16
			terns							
O. Piciformes										
F. Picidae	-	-	*Picoides*	-	-	*P. borealis*	-	-	0.140	29
SF. Jynginae						red-cockaded woodpecker				
	-	-	*Sphyrapicus*	0.007	0.000-0.023	-	-		0.053	18
			sapsuckers							
	-	-	*Colaptes*	-	-	*C. auratus*	0.014	-	0.042	14
						Northern flicker				
O. Passeriformes										
F. Tyrannidae	0.145	0.044-0.384	*Empidonax*	0.126	0.044-0.384	-	-	-	-	32
SF. Elaeniinae			flycatchers							
	-	-	*Empidonax*	0.007	0.000-0.023	-	-	-	-	25
			flycatchers							
F. Paridae	-	-	*Parus*	-	-	*P. bicolor*	-	0.063	-	6
						tufted titmouse				

Literature values of Nei's (1978) genetic distance (D) and Wright's F_{ST} values for various avian species found in North America cont.

Taxonomic Classification	D w/in subfamily		D w/in genera			D between subspp. or between local* populations			F_{ST}	Ref[1]
	mean	range	Genus	mean	range	species	mean	range		
O. Passeriformes F. Muscicapidae SF. Turidinae	0.251	0.010-0.622	*Catharus* thrushes	0.024	0.010-0.028	-	-	-	-	2
F. Mimidae	-	-	*Toxostoma* thrashers	0.080	0.069-0.090	-	-	-	-	5
F. Sturnidae SF. Sturininae	-	-	*Sturnus*	-	-	*S. vulgaris* European starling	0.0024*	0.000-0.005	0.038	24
F. Vireonidae SF. Vireoninae	-	-	*Vireo* vireos	0.287	0.027-0.520	-	-	-	-	5
O. Passeriformes F. Emberizidae SF. Parulinae	0.258	0.052-0.693	*Dendroica* wood warblers	0.050	0.000-0.165	-	-	-	-	4
	0.179	0.050-0.400	*Dendroica*	0.100	0.000-0.150	-	-	-	-	10
	-	-	*Dendroica*	-	-	*D. coronata* yellow-rumped warbler	0.002*	0.000-0.008	0.005	9
	-	-	*Vermivora* wood warblers	0.001	-	-	-	-	0.011	13
	-	-	*Geothlypis* yellowthroats	0.006	-	-	-	-	0.040	34
SF. Emberizinae	0.240	0.024-0.636	sparrows	-	-	-	-	-	-	3
	0.246	0.028-0.445	*Zonotrichia*	0.117	0.028-0.196	-	-	-	-	31
	-	-	*Zonotrichia*	-	-	*Z. leucophrys* white-crowned sparrow	0.008	0.000-0.025	0.056	12

Literature values of Nei's (1978) genetic distance (D) and Wright's F_{ST} values for various avian species found in North America cont.

Taxonomic Classification	D w/in subfamily		D w/in genera			D between subspp. or between local* populations			F_{ST}	Ref[1]
	mean	range	Genus	mean	range	species	mean	range		
O. Passeriformes F. Emberizidae SF. Emberizinae cont	-	-	*Zonothrichia*	-	-	*Z. capensis* rufous-collared sparrow	-	-	0.118	21
	-	-	*Amphispiza*	-	-	*A. belli* sage sparrow	0.005	0.008-0.027	0.112	19
SF. Icterinae	0.226	0.011-0.451	blackbirds	-	-	-	-	-	-	27
	-	-	*Quiscalus* grackles	0.001	-	-	-	-	-	6
	-	-	*Icterus*	-	-	*I. galbula* Northern oriole	0.003	0.001-0.006	-	11

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