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GENETIC DIVERGENCE AMONG POPULATIONS OF THE HAWAIIAN DUCK, LAYSAN DUCK, AND MALLARD

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ABSTRACT.—Allozymic variation at 20 gene loci was estimated for populations of the Laysan Duck (*Anas laysanensis*) and the Hawaiian Duck (*A. wyvilliana*) from the Hawaiian archipelago, as well as for Mallard populations (*A. platyrhynchos*) from Hawaii and North America. The Laysan Duck and Hawaiian Duck are endemic, have experienced severe bottlenecks, and are listed as endangered species. Alternative alleles are fixed at six loci for Mallards versus Hawaiian anatids (Hawaiian and Laysan ducks). In contrast, every allelic variant found in the Laysan Duck was present in the Hawaiian Duck (but not vice versa), suggesting the former is an offshoot of the latter. The genetic distance (Nei's *D*) between Laysan and Hawaiian ducks is less than 0.01, while that between both Hawaiian and Laysan ducks and Mallards is greater than 0.45. The allozymic evidence also suggests that there has been extensive hybridization between Mallards and Hawaiian Ducks on Oahu, with the near disappearance of Hawaiian Duck alleles. However, there is only slight evidence of Mallard genic introgression into the Hawaiian Duck population on Kauai. Finally, the allozymic data suggest that the Hawaiian Duck is a distinct species from the Mallard, but that little genetic divergence has occurred between Hawaiian and Laysan ducks. *Received 25 July 1991, accepted 8 March 1992.*

THE RESULTS of evolutionary processes on oceanic islands are evident in the Hawaiian avifauna, which exhibits striking examples of adaptive radiation. Hawaii provides a model system to examine the genetic divergence of an endemic, insular waterbird fauna. Several of these waterbird species have gone through severe population bottlenecks and have remained at chronically small populations (Scott et al. 1986). Of the relatively few avian families that colonized the remote Hawaiian archipelago, waterbirds were further restricted by the scarcity of coastal and inland wetlands in the islands (Griffin et al. 1989). Today, three endemic waterbird species survive: the Hawaiian Goose (*Nesochen sandivicensis*), Hawaiian Duck (*Anas wyvilliana*), and Laysan Duck (*A. laysanensis*). All are believed derived from North American species. However, the phylogeny of the Hawaiian waterbirds is not well established and is based primarily on characters such as bill size, plumage color, and plumage pattern.

Approximately 3,200 Hawaiian Ducks occur on the islands of Hawaii, Oahu and Kauai, whereas the Laysan Duck has an estimated population of 500 (Griffin et al. 1989) and is limited solely to Laysan Island (Fig. 1). Both species historically have experienced severe population bottlenecks. Furthermore, reestablishment and maintenance of populations of Hawaiian Ducks on Oahu and Hawaii relied on progeny from relatively few captive-reared birds. Thus, genetic diversity of these species may be substantially reduced (Griffin et al. 1989).

The Hawaiian Duck, Laysan Duck and Mariana Mallard (*A. oustaleti*) are monochromatic, insular endemics that presumably evolved from stray migratory Mallard (*A. platyrhynchos*) stocks (Weller 1980). Currently, the AOU *Check-list* (1983) classifies the Hawaiian Duck as a distinct species, but birds in this taxon sometimes have been classified as a subspecies of the Mallard (Delacour 1956, Weller 1980). The Hawaiian Duck is listed as endangered by the U.S. Department of the Interior and the state of Hawaii.

Formerly, the Hawaiian Duck occupied all the main Hawaiian Islands except Lanai and Kahoolawe (Perkins 1903; see Fig. 1). Numbers declined noticeably after the turn of the century (Swedberg unpubl. manuscript). By 1960, the species was found only on Kauai with an estimated 3,000 ducks on the island in the mid-1960s (Swedberg unpubl. manuscript). A captive propagation and release program for the Hawaiian Duck was initiated in 1958, and birds subsequently were released on Hawaii and Oahu (Paton 1981, U.S. Fish Wildl. Serv. 1985). Over 500 captive-reared Hawaiian Ducks have been

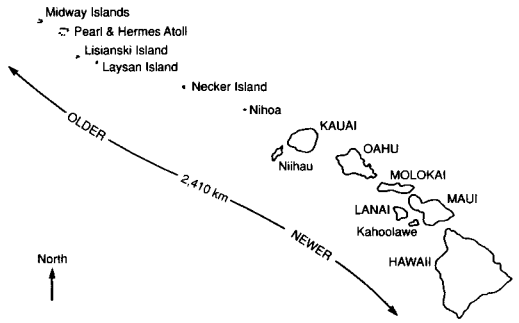

Fig. 1. The Hawaiian Islands.

released on Oahu since 1968 (Bostwick unpubl. manuscript). Fewer than 300 have been counted during semiannual statewide counts since 1980 (Griffin et al. 1989). There is potential for hybridization of Hawaiian Ducks with feral Mallards on the three islands where Hawaiian Ducks are believed to occur (Griffin et al. 1989).

Having the most restricted distribution of any extant species of duck, the Laysan Duck is restricted to the 400-ha Laysan Island in the northwestern Hawaiian Islands (Fig. 1). It was reported to also inhabit Lisianski Island in 1828, a 170-ha island over 230 km northwest of Laysan but it no longer occurs there (Berger 1981). The number of Laysan Ducks has fluctuated dramatically, from 7 birds in 1912 to 500 in the 1960s (Berger 1981). However, as few as 25 were seen in 1973 and as many as 350 were counted in 1978 (Sincock and Kridler unpubl. manuscript), suggesting that several population bottlenecks occurred. In 1979, the Laysan Duck population was estimated at 500 (Moulton and Weller 1984). In addition, a captive population has been maintained since the early 1960s and currently numbers 22 ducks. No reintroductions to the wild population have been made from captive-reared stock (J. G. Giffin pers. comm.).

To date, Hawaiian and Laysan duck populations have been characterized solely by classical taxonomic methods. The objectives of this study are to: (1) quantify the degree of genetic variation and differentiation within and among endangered Hawaiian and Laysan ducks, and their presumed ancestral populations (represented by samples of Mallards from Oahu and California); (2) evaluate the degree of interspecific hybridization among Hawaiian Ducks and Mallards; (3) assess the potential significance of introgressive hybridization by Mallards on the species integrity of the Hawaiian Duck; (4) quantify the degree of genetic variability within and among captive flocks of Hawaiian and Laysan ducks.

Materials and Methods

Samples of tissues were taken from January 1988 through November 1989 from wild birds and captive birds, and nonlethal collection of blood and feather pulp from captive birds. Sample sizes were limited due to the endangered status of the Hawaiian anatids. Samples were obtained as follows: (1) For Mallards, tissue samples (heart, kidney and liver) were obtained from six wild Mallards from Oahu collected from Paradise Park and Kahuku Meadow Gold Dairy. Tissue samples were also taken from six wild, suspected Hawaiian Duck/Mallard hybrids collected from the Kii Unit of James Campbell National Wildlife Refuge (NWR) in Oahu. Body size and plumage characteristics (especially head coloration for males) were the criteria used to identify suspected hybrids. Tissue was also obtained from 11 eggs collected from 11 wild duck nests at the Kii Unit of James Campbell NWR. The parental pairs which laid the eggs were suspected to be Hawaiian Duck/Mallard hybrids. Tissue sam-

TABLE 1. Allele frequencies of at 11 loci for Laysan Duck, Hawaiian Duck and Mallard populations.

	Est-1		Idh-1		Lap-1		Ldh-1		Pep-1		Pep-2	
	75	100	50	100	100	NP[a]	75	100	80	100	88	94
Laysan Ducks (C[b])		1.00		1.00	1.00			1.00		1.00	0.29	0.71
Hawaiian Ducks (C[b])	0.12	0.88		1.00	1.00		0.38	0.62	0.17	0.83	0.33	0.63
Hawaiian Ducks (W[c])		1.00		1.00	1.00			1.00	0.19	0.81	0.06	0.94
NC Mallard (C[b])	0.50	0.50	1.00			1.00		1.00	1.00			1.00
CA Mallard (W[c])	0.96	0.04	1.00			1.00		1.00	1.00		0.08	0.92
Oahu Mallards (W[c])	0.75	0.25	1.00			1.00		1.00	1.00			1.00
Oahu possible hybrids (W[c])	0.75	0.25	0.67	0.33	0.33	0.67		1.00	0.75	0.25	0.25	0.75
Eggs (possibly hybrids)	0.50	0.50									0.25	0.75

[a] NP = not present.
[b] C = captive.
[c] W = wild.

ples were taken from 13 wild Mallards collected from two different sites approximately 25 km apart in central California (Sutter and Delevan NWR). Tissue samples were also obtained from one Mallard from a private captive flock in North Carolina. (2) For Hawaiian Ducks, tissue samples were taken from 12 Hawaiian Ducks from the Pohakuloa Endangered Species Propagation Facility on Hawaii, as well as from a recently deceased Hawaiian Duck on Kauai. Feather pulp and blood samples were obtained from seven wild Hawaiian Ducks captured at Hanalei NWR on Kauai that were in captivity at Olinda Endangered Species Propagation Facility on Maui. (3) For Laysan Ducks, tissue samples were obtained from seven Laysan Ducks from the Pohakuloa Endangered Species Propagation Facility.

Samples were frozen at −70°C and, subsequently, shipped by air to Wake Forest University on dry ice or liquid nitrogen and stored at −70°C for analyses, except for the North Carolina Mallard where no sample transport was required. Tissues were homogenized by mortar and pestle at 4°C with equal amounts (vol/vol) of buffer with 1% NADP and centrifuged at 6,000 × *g* for 5 min. The supernatant was stored at −70°C until used for starch-gel electrophoresis.

Allozymic analyses were conducted on tissue or blood and feather pulp (Marsden and May 1984) from 53 birds and 11 eggs. To our knowledge, none of the birds were related, although the birds from the captive facility presumably have a relatively high inbreeding coefficient. Following the techniques of Browne (1988) and Browne and Hoopes (1990), we surveyed 15 enzyme systems representing the following 20 loci: Aco-1, Adh-1, Est-1, Est-2, Got-1, G-6pdh, Idh-1, Lap-1, Ldh-1, Mdh-1, Mdh-2, Pep-1, Pep-2, Pgi-1, Pgm-1, Pgm-2, Sdh-1, Sod-1, Xdh-1, Xdh-2. Peptidases 1 and 2 were resolved using Leu-Gly-Gly as the substrate. Homogenates from frozen tissues and blood were used for horizontal starch gel (12%) electrophoresis. Two buffer systems were used: tris-EDTA-boric acid; and Poulik and Bearn's (1962) discontinuous tris-citrate. All gels are currently stored in the senior author's laboratory.

For each electrophoretically detectable locus, the mobility (distance traveled) of the fastest-moving allelic product found was used as the standard and designated 100. Other alleles were designated by the migration distance of their protein products to that of allele 100. Multiple loci encoding the same enzymatic activity were numbered sequentially beginning with the form migrating closest to the origin. The percentage of polymorphic loci was calculated as the number of loci polymorphic divided by the total number of loci examined. Heterozygosity was defined as the number of heterozygous genotypes recorded in a sample divided by the product of the number of loci and the number of individuals assayed. Genetic distance was calculated using Nei's (1978) unbiased *D*. Only those loci where alternate allelic states could be identified were used in the calculations of *D* (i.e. Lap-1, Pgm-2, and Xdh-2 were not used in estimating *D* since no enzyme actively was detectable in some of the populations).

Results

No protein variability was found for nine loci (Aco-1, Adh-1, Est-2, Got-1, G-6pdh, Mdh-1, Mdh-2, Pgm-1, and Sdh-1). At six loci (Idh-1, Lap-1, Pgm-2, Sod-1, Xdh-1, and Xdh-2), alternate alleles are fixed for Mallards versus Hawaiian and Laysan ducks (Table 1). In contrast, Hawaiian and Laysan ducks share the same alleles at the six indicator loci. From the allozymic data, those populations are virtually indistinguishable (Table 1).

Lap-1 and Xdh-2 were present in Hawaiian anatids but were not detected in Mallards, while Pgm-2 was present in Mallards but not in Hawaiian Ducks. It is possible that the alleles are present in the samples but not at detectable levels or that the enzyme had degraded prior to electrophoresis. The latter is considered unlikely since enzymatic activity of the other loci

TABLE 1. Extended.

Pep-2	Pgi-1		Pgm-2		Sod-1		Xdh-1		Xdh-2	
100	50	100	100	NP[a]	69	100	50	58	100	NP[a]
	1.00			1.00		1.00	1.00		1.00	
0.04	1.00			1.00		1.00	1.00		1.00	
	0.88	0.12		1.00		1.00	1.00		1.00	
		1.00	1.00		1.00			1.00		1.00
		1.00	1.00		1.00			1.00		1.00
		1.00	1.00		1.00			1.00		1.00
	0.25	0.75	0.83	0.17	0.83	0.17		1.00		1.00
			1.00		1.00			1.00		1.00

TABLE 2. Genotype frequencies at 11 loci for Laysan Ducks, Hawaiian Ducks and Mallard populations.

		Est-1			Idh-1		Lap-1		Ldh-1			Pep-1			Pep-2		
				75/						75/			80/				
	n	75	100	100	50	100	100	NP[a]	75	100	100	80	100	100	88	94	100
Laysan Ducks (C[b])	7	0	7	0	0	7	7	0	0	7	0	0	7	0	1	4	0
Hawaiian Ducks (C[b])	12	0	9	3	0	12	12	0	4	7	1	1	9	2	3	6	0
Hawaiian Ducks (W[c])	8	0	8	0	0	8	8	0	0	8	0	0	5	3	0	6	0
NC Mallard (C[b])	1	0	0	1	1	0	0	1	0	1	0	1	0	0	0	1	0
CA Mallard (C[b])	13	12	0	1	13	0	0	13	0	13	0	12	0	1	0	11	0
Oahu Mallards (C[b])	6	3	0	3	6	0	0	6	0	6	0	6	0	0	0	6	0
Oahu possible hybrids (C[b])	6	4	1	1	4	2	2	4	0	6	0	4	1	1	1	4	0
Eggs (possible hybrids)	11	4	4	3											1	7	0

[a] NP = not preesnt.
[b] C = captive.
[c] W = wild.

showed no degradation and because the results were consistent within Mallards and within Hawaiian anatids despite different collection times and handling procedures.

Four of the six suspected hybrid ducks collected from the Kii Unit of James Campbell NWR on Oahu are predominantly Mallard genotypes (Table 2). The other two ducks collected on Oahu appear to be Hawaiian Duck/Mallard hybrids as indicated by the frequency of the Hawaiian Duck/Laysan alleles at Idh-1, Lap-1, Pep-1, Pep-2, Pgm-1 and Sod-1 (Table 1). Similarly, the allozymes from eggs obtained from the Kii Unit also appear to be predominantly Mallard allozymes, with Mallard alleles fixed at the Xdh-1 and Xdh-2 loci for all 11 eggs.

For the seven wild Hawaiian Ducks from Kauai, some differences were found between feather pulp and blood samples (from the same individual). Est-1 appeared only in blood samples and Lap-1 stained more intensely in blood. Idh-1 and Pgi-1 appeared only in quill samples. Sdh-1 did not appear in either quill or blood, but because it was monomorphic in all other populations and in one wild Kauai Hawaiian Duck for which heart and kidney tissue were obtained, we presume it was monomorphic in all populations. Differences between quill and blood samples with regard to loci detection are similar to those reported by Marsden and May (1984).

Many enzymes were not detectable in egg samples (Table 2). While there was no difference in Mdh-1 between Mallards and Hawaiian anatids (and among almost all bird species; Barrowclough 1983), an alternate form occurred in eggs (mobility = 108) than in adults (100). This suggests ontogenetic changes in allele frequencies as has been reported in other organisms such as *Drosophila* (Bewley 1983).

In contrast to ducks collected on Oahu, the wild Hawaiian Ducks sampled from Kauai are predominantly Hawaiian Duck genotypes (Table 2). Yet, the occurrence of Mallard alleles at the Pgi-1 locus for one of the eight Hawaiian Ducks suggests some hybridization with Mallards (Table 1).

Calculations of percent of loci polymorphic (%*P*) and average individual heterozgosity ($\bar{H}$) for the Laysan Duck, Hawaiian Duck and Mallard populations (Table 3) indicate that Hawaiian Ducks are more than three times as polymorphic as Laysan Ducks. In addition, every allelic variant present in Laysan Ducks is present in Hawaiian Ducks (Table 1) but not vice versa, suggesting that the Laysan Duck population is an offshoot of the Hawaiian Duck population. Further, the captive Hawaiian Ducks

TABLE 3. Estimates of genetic variability in Laysan Duck, Hawaiian Duck and Mallard populations.

	Percent loci polymorphic (% *P*)	$\bar{H}$[a]
Laysan Duck	5	0.014
Hawaiian Duck (C[b])	20	0.038
Hawaiian Duck (W[c])	15	0.032
Mallard (North Carolina)	5	0.050
Mallard (California)	15	0.015
Mallard (Oahu)	5	0.025
Potential hybrid (Oahu)	40	0.033
Hawaiian Duck (C[b] + W[c])	25	0.035
Mallard (All[d])	15	0.020

[a] $\bar{H}$ = average individual heterozygosity.
[b] C = captive.
[c] W = wild.
[d] All = North Carolina, California, and Oahu.

TABLE 2. Extended.

Pep-2		Pgi-1			Pgm-2		Sod-1		Xdh-1		Xdh-2	
88/94	94/100	50	100	50/100	100	NP[a]	69	100	50	58	100	NP[a]
2	0	7	0	0	0	7	0	7	7	0	7	0
2	1	12	0	0	0	12	0	12	12	0	12	0
1	1	7	1	0	0	8	0	8	8	0	8	0
0	0	0	1	0	1	0	1	0	0	1	0	1
2	0	0	13	0	13	0	13	0	0	13	0	13
0	0	0	6	0	6	0	6	0	0	6	0	6
1	0	1	4	1	5	1	5	1	0	6	0	6
3	0				11	0	11	0	0	11	0	11

and wild Hawaiian Duck populations each represent a fraction of the genetic variation present in Hawaiian Ducks; that is, they are genetic subsets of the entire Hawaiian Duck population. The high level of polymorphism found in the suspected hybrids is due to the presence of allelic variants inherited from the parental species (Mallards and Hawaiian Ducks). Finally, although the degree of polymorphism has high variability among the populations (range 5 to 40%), $\bar{H}$ is relatively constrained (range 0.014 to 0.05).

Several observations can be made from calculations of genetic identities and genetic distances among the populations (Table 4). First, the number of allelic substitutions between the Laysan Duck and Hawaiian Duck populations is less than 1 per 100 loci (Table 4). The genetic distance between the captive and wild Hawaiian Ducks is also low, with less than 1 allelic substitution per 100 loci. The genetic distance between Hawaiian anatids and Mallards ranges from 0.361 to 0.459, with more genetic divergence between Hawaiian anatids and Mallards than between Laysan and Hawaiian ducks. Finally, although not included in Table 4, the genetic distance between the Mallard–Hawaiian Duck hybrids and Oahu Mallards is 0.053, and between the hybrids and wild Hawaiian Ducks is 0.209, indicating that the hybrids are primarily Mallard genotypes.

DISCUSSION

Our study of genetic difference between Mallards and Hawaiian anatids indicates two distinct gene pools. The first consists of the Hawaiian and Laysan ducks, while the second includes Mallards from Oahu, California and North Carolina. Thus, Hawaiian Ducks are distinct genetically from Mallards and warrant full phylogenetic species status based on allozymic evidence. In contrast, there is a high degree of genetic similarity between Hawaiian and Laysan ducks, with the two species virtually indistinguishable based on the alleles examined. Barrowclough (1983), Gutierréz et al. (1983) and Johnson and Zink (1983) argued that genetic distance per se between two taxa does not indicate their taxonomic status. We agree, since taxonomic status requires information about mating preferences, behavior, and hybrid fit-

TABLE 4. Genetic identities (above diagonal) and genetic distance (below diagonal) for populations of Laysan Ducks, Hawaiian Ducks and Mallards.

		Hawaiian Duck		Mallard	Mallard
	Laysan Duck	C[a]	W[b]	(California)	(Oahu)
Laysan Duck		0.988	0.994	0.639	0.655
Hawaiian Duck (C[a])	0.012		0.991	0.650	0.667
Hawaiian Duck (W[b])	0.006	0.008		0.631	0.697
Mallard (California)	0.448	0.413	0.459		0.992
Mallard (Oahu)	0.423	0.404	0.361	0.007	

[a] C = captive.
[b] W = wild.

ness. Nevertheless, the lack of any allelic variation in Laysan Ducks that was not present in Hawaiian Ducks suggests an extremely close relationship between Laysan and Hawaiian ducks.

Our allozymic data for the Mallard populations are similar to those of Ankney et al. (1986) for most loci that were jointly examined. The only notable exception is that they reported data for a single PGM locus, while we found an additional (faster migrating) locus. The heterozygosity level reported by Ankney et al. (1986) also was higher than our values ($\bar{H}$ = 7.6% vs. 1.5%), but we did not examine some of the variable loci reported by Ankney et al. (1986). Our values are closer to those reported for Mallards by Parker et al. (1981; $\bar{H}$ = 2.7%) and Patton and Avise (1986; $\bar{H}$ = 3.7%). Some additional differences exist between our results and the latter, principally with regard to whether loci were monomorphic or polymorphic. These differences are not unusual given the relatively small sample sizes of both studies. Since the geographical origin of the Mallards used by Patton and Avise (1986) was not listed, differences in allele frequencies may also be due to sampling error.

Barrowclough (1983) reviewed the biochemical studies of microevolutionary processes in birds. For 30 bird species, $\bar{H}$ ranged from 0.007 to 0.147, with mean heterozygosity of 0.053. The values from our study are within this range. Heterozygosity levels for Hawaiian anatids are approximately the same as those of Mallard populations. Although bottlenecks have been reported for Hawaiian anatids, they may not have occurred with enough frequency or severity to decrease heterozygosity. Soulé (1980) suggested that bottlenecks must occur frequently to cause seriously decreased heterozygosity. If the Hawaiian Islands were colonized by ancestral Mallard stock millions of years ago, founder events may have resulted in loss of heterozygosity, which subsequently has been restored through mutation.

The mean genetic distance between Mallard populations from Ontario, Manitoba and Saskatchewan, Canada and the Sacramento delta area of California reported by Ankney et al. (1986) was 0.0010, while the mean genetic distance among three Black Duck (*A. rubripes*) and four Mallard populations was 0.0006. Patton and Avise (1986) found a similar value of 0.001 for smaller samples of Mallards and Black Ducks. Small genetic distances are characteristic of local populations of avian species in many orders (reviewed in Ankney et al. 1986). Thus, the *D*-values we report between populations of Hawaiian anatids, or between populations of Mallards, are within the range found in past studies. Data compiled by Avise (1983) revealed that the level of protein divergence in avian congeners is conservative compared to most nonavian congeners. There are numerous explanations for this difference (see Avise 1983), but one possibility is that avian congeners are evolutionarily younger than most nonavian congeners. This could be due to excessive "splitting" at the genus level by avian systematists. In contrast, a *D*-value of 0.459 between Hawaiian anatids and Mallards suggests a long history of isolation and lack of gene flow. The value is higher than those reported for past studies; however, congeneric genetic divergence among vireos has been reported to be more extensive (D = 0.56; Avise 1983).

The results suggest that Hawaiian anatids are not genetically similar to Mallards. The genetic distance of 0.459 between Hawaiian anatids and Mallards exceeds the largest *D*-value (0.19) among the 10 *Anas* species reported by Patton and Avise (1986). A number of factors can affect estimates of genetic distance. The large genetic distance we found is primarily due to alternately fixed alleles in Mallards and Hawaiian anatids (Table 1). However, since no enzyme activity was detected for Lap-1, Pgm-2, and Xdh-2, data from these loci were not included in the calculations of genetic distance. Three loci (Lap-1, Xdh-1 and Xdh-2) were not reported by Patton and Avise (1986) or Ankney et al. (1986). In our study, LAP was also not detectable in Mallards but was easily scorable in Hawaiian anatids. This may explain why LAP was not reported in the other *Anas* studies. We found that Idh-1 occurred as alternately fixed alleles in Hawaiian anatids and Mallards, while Idh-1 was reported to occur as two morphs (100 and 200 mobility) in approximately equal frequencies in Mallards by Patton and Avise (1986). However, it was reported to be monomorphic in a California sample of Mallards and nearly monomorphic (159/160) in a Canadian sample (Ankney et al. 1986). Sod-1 occurred as alternately fixed alleles in our study. It was not reported by Patton and Avise (1986), but the most common allele comprised 93% of a California sample of Mallards (Ankney et al. 1986).

Since our genetic distances exceeded those previously reported between *Anas* species, new

homogenates were processed from the original tissues to check for possible degradation of the original samples. No notable difference in allelic variants was found between the newly processed samples and the original samples. Samples were also electrophoresed on both TBE and Poulik's buffers. Thus, almost all samples were electrophoresed, stained and scored for alloyzmic frequencies on two separate occasions.

Given their morphological similarity and evidence for hybridization (resulting in at least F_1 production), Mallards appear to be the likely ancestral stock of Hawaiian anatids. The high level of genetic divergence may be due to stochastic factors, such as genetic drift. Barrowclough (1983) speculated that the reduced genetic distances among avian populations of the same species and among conspecifics (compared to other vertebrates) is due to the greater vagility of birds. However, the Hawaiian Islands are the most isolated archipelago in the world. The populations potentially were founded by only a few individuals, with possibly no subsequent immigration until very recently. Hawaiian Ducks have colonized a number of distant islands and are known to have experienced severe bottlenecks, perhaps repeatedly. In general, speciation in populations with a genetic structure consisting of small demes will be associated with large genetic distances (Templeton 1980a, b, Barrowclough 1983). Thus, it is not surprising that the genetic distances between Hawaiian anatids and Mallards are considerably higher than those reported for most other avian congeners.

Laysan Ducks have the lowest genetic variability of the populations examined in this study, probably reflecting the numerous population bottlenecks the species has experienced both in the wild and captivity. It is surprising that Mallards have as low genetic variability (measured by percent of loci polymorphic or $\bar{H}$) as Hawaiian and Laysan ducks, especially since Mallards were sampled from both California and Oahu. Some factors that may explain this low variability are: (1) the Oahu Mallard population originated from California; (2) all California samples come from approximately the same area and were collected at the same time; (3) Mallards have low variability.

Our data on the degree of interspecific hybridization of wild Hawaiian Duck and Mallards on Oahu indicate that a genetically intact Hawaiian Duck population probably does not exist on this island. Ducks and eggs collected from the Kii Unit also clearly exhibited Mallard genotypes. Although we have no data on duck populations on the island of Hawaii, we suspect that a genetically intact Hawaiian Duck population probably does not persist on this island. Because there are relatively few wetland habitats on this island, only a relatively small number of captive-reared Hawaiian Ducks have been released (361 ducks from 1958–1979; J. Giffin pers. comm.), and Mallards are common. In contrast, allozymic data from ducks sampled from Kauai indicate that a genetically intact Hawaiian Duck population persists on this island. However, the occurrence of one possible hybrid bird in this sample suggests that introgressive hybridization by Mallards may be occurring within the Kauai Hawaiian Duck population. Note that all but one of the eight Kauai ducks sampled were obtained from Hanalei NWR, a lowland waterbird refuge and an area that presumably is susceptible to Mallard infiltration.

The potential for gene flow among Hawaiian Ducks and Mallards is high for several reasons. First, the frequency of interspecific hybridization within the Anatidae is high (Scherer and Hilsberg 1982). Second, since the 1960s, large numbers of domesticated Mallards have moved into the wild on Oahu (Bostwick 1982). Third, the potential for contact between the two species is high considering that there are relatively few suitable duck-nesting habitats available on Oahu (Griffin et al. 1989) and that there is a scarcity of conspecific mates on the island. Fourth, there is the inevitability of forced copulations with Hawaiian Ducks by the larger, more aggressive Mallards.

To understand fully the large genetic distances between Hawaiian anatids and Mallards, additional work is required, including estimates of genetic divergence for the Mariana Mallard from Mallards and from Hawaiian anatids. Other techniques, such as mtDNA or nuclear-DNA sequence analysis, would yield independent estimates of genetic divergence. Hybridization tests, focusing especially on F_2 fertility, would be instructive. Finally, estimates of genetic divergence for other geographically isolated avian species (e.g. Galapagos finches) from their presumed ancestral stock also are needed.

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