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GENETIC ANALYSES OF WILD POPULATIONS OF HAWAIIAN GEESE USING DNA FINGERPRINTING[1]

ELIZABETH H. RAVE[2]
Department of Biology, University of North Dakota, Grand Forks, ND 58202 and Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, DC 20008

Abstract. DNA fingerprinting was used to compare levels of genetic variation among 75 wild Hawaiian Geese, or Nene (*Branta sandvicensis*), from six populations on the islands of Hawaii, Maui, and Kauai and between the six wild populations and a captive colony of 29 Nene. Mantel tests were used to determine differences in similarity coefficient distributions (amount of genetic similarity among individuals within each population) among wild Nene and between wild and captive Nene. Nene from Hawaii Volcanoes National Park on the island of Hawaii had the lowest similarity coefficient distribution, whereas Nene on Kauai had the highest. Captive birds had an intermediate similarity coefficient distribution when compared to wild populations. No unique DNA fingerprint fragments were found in wild birds when compared to captive birds. Successful recruitment of migrants might have decreased similarity at Hawaii Volcanoes National Park, whereas inbreeding and captive-release techniques might have increased similarity on Kauai. Varying levels of inbreeding or fixation by drift might explain differences in similarity coefficient distributions between wild and captive populations.

Key words: Branta sandvicensis; *DNA fingerprinting; Hawaiian Goose; Nene; population genetics.*

INTRODUCTION

DNA fingerprinting, which involves comparisons of hypervariable minisatellite DNA sequences (Jeffreys et al. 1985a, Burke 1989), is used increasingly in studies designed to document the genetic structure of wild populations (Faulkes et al. 1990; Gilbert et al. 1990; Reeve et al. 1990; Triggs et al. 1991, 1992; Wayne et al. 1991). As population size is reduced, genetic diversity is expected to decrease (Wright 1931, Nei et al. 1975). Such losses of heterozygosity and allelic diversity result from genetic drift (Fuerst and Maruyama 1986) and inbreeding (Wright 1931, Nei et al. 1975) within small populations. Low genetic diversity may adversely affect individual fitness (Ralls and Ballou 1983, Templeton and Read 1983, Allendorf and Leary 1986), whereas high genetic diversity may increase the potential for future evolutionary adaptation (Frankel and Soulé 1981). DNA fingerprinting can be used to reveal genetic variation and is, therefore, a useful technique for biologists who must determine optimal management strategies for small, wild populations.

The endangered Hawaiian Goose, or Nene (*Branta sandvicensis*), underwent a severe population bottleneck, from an estimated 25,000 birds during the late 18th century (Baldwin 1945) to only 17 individuals known by 1950 (Elder and Woodside 1958). Only through numerous releases of captive-bred birds did wild Nene populations recover (Kear and Berger 1980, Black et al. 1991). Although genetic variation of captive Nene used in the propagation and release program has been documented (Rave et al. 1994), no information on wild birds is available.

To further enhance genetic management practices of both wild Nene and captive Nene destined to be released, genetic assessment of wild populations is necessary. Therefore, I used DNA fingerprinting to compare levels of genetic variation among six wild populations of Nene on the islands of Hawaii, Maui, and Kauai. I also compared wild Nene with Nene from one captive colony to determine genetic differences among the populations and to determine the presence of unique fingerprint fragments in wild birds not currently found in the captive birds' gene pool. If unique fragments are found, the wild individuals can be captured and used in the propagation

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[2] Present address: Department of Biology, Bemidji State University, Bemidji, MN 56601.

effort to increase the genetic variation of captive-released birds.

STUDY SPECIES AND AREA

Nene typically inhabit high-elevation areas (1,200–2,200 m) on Hawaii and Maui (Stone et al. 1983) and low-elevation areas (sea level to 300 m) on Kauai (T. Telfer, pers. comm.). Lowland habitat was likely important to all prehistoric and historic Nene populations (Stone et al. 1983). Fossil bones have been found at or near sea level (Olson and James 1982), and altitudinal migrations were common (Henshaw 1902). However, habitat destruction and the introduction of plants and animals modified lowland habitats and contributed to the population decline of Nene. By the late 1800s, Nene were rare on Hawaii and extinct on Maui and Kauai (Baldwin 1945).

To increase numbers of wild Nene, two captive colonies were established from the same genetic stock, one in Pohakuloa, Hawaii (now Olinda, Maui) in 1949, and a second in Slimbridge, England in 1950 (Kear and Berger 1980). The goal of these colonies was to rear birds in captivity for eventual release into the wild, thereby restoring self-sustaining populations to Hawaiian ecosystems (Stone et al. 1983). Beginning in 1960, Nene from Pohakuloa were released on Hawaii and Maui, and Nene from Slimbridge were released on Maui (Kear and Berger 1980). Captive releases ceased on Maui in 1981 (Black et al. 1991), but Nene from Olinda are still released yearly on Hawaii. Although over 2,100 Nene have been released since 1960, population numbers are estimated at only 339 birds on Hawaii; however, numbers on Maui have remained stable at approximately 184 birds (Black et al. 1991).

In 1982, a flock of 12 Nene established itself on Kauai (Black and Banko 1994). This flock descended from the same genetic stock as the two captive colonies (F. Duvall, pers. comm.). Beginning in 1991, Nene from Olinda have been released yearly on Kauai to increase genetic diversity and facilitate population expansion. In 1994, population numbers were estimated at 130 birds (T. Telfer, pers. comm.), almost 11 times more than the original flock numbers.

My study sites included six populations on three islands: Hawaii Volcanoes National Park (HVNP), Kahuku, Keaau, and Puuwaawaa on Hawaii, Haleakala National Park on Maui, and Waiopili Spring on Kauai (Fig. 1). HVNP extends from sea level to the summit of Mauna Loa (4,145 m) and supports the largest number of birds on the island (Black et al. 1991). Nene are found throughout much of the park, from vegetatively sparse volcanic substrates to pastures and even a golf course. Kahuku is a privately owned ranch on the southeastern slope of Mauna Loa and extends from 600–2,100 m. Nene are found in lowland pastures and upland montane scrubland. The Keaau population originated in 1984 (Black et al. 1991), when captive Nene from Pohakuloa were culled and released here (F. Duvall, pers. comm.). Keaau is located at sea level on the eastern shore of Hawaii and is characterized by irrigated pastures with fresh grass available to Nene throughout the year (Black et al. 1991). Puuwaawaa, which is part of the Keauhou II Sanctuary population, is located north of Mt. Hualalai on the western side of Hawaii. Puuwaawaa is also a privately owned ranch and is located at 725 m. A man-made reservoir attracts Nene, and a regularly mowed lawn provides Nene with food throughout the year (J. Mello, pers. comm.).

Haleakala National Park supports the only population of Nene on Maui. Most of these birds are located inside Haleakala Crater at approximately 2,000 m. The western end of the crater is dry, with progressively more rainfall and vegetation toward the east (Kear and Berger 1980). Nene habitat on Maui has less grazing pressure, more intensive predator control, and higher rainfall than habitat on Hawaii (Black et al. 1991, Banko 1992).

Waiopili Spring, near the town of Koloa, is located on the southeastern coast of Kauai. This area supports only part of the Nene population, which is distributed along the eastern side of the island. Nene are found at low elevations and spend the majority of their time on irrigated pastures (Black et al. 1991). Unlike Hawaii and Maui, Kauai has no mongooses (*Herpestes auropunctatus*), a major predator of Nene eggs and goslings on other islands (Baldwin 1945, Stone et al. 1983, Banko 1992).

METHODS

I collected 1–2 ml of whole blood from 31 wild Nene from HVNP (19% of the estimated population), 3 from Kahuku (10% of population), 10 from Keaau (25% of population), 12 from Puuwaawaa (40% of population), 14 from Maui (8% of population), and 5 from Kauai (9% of

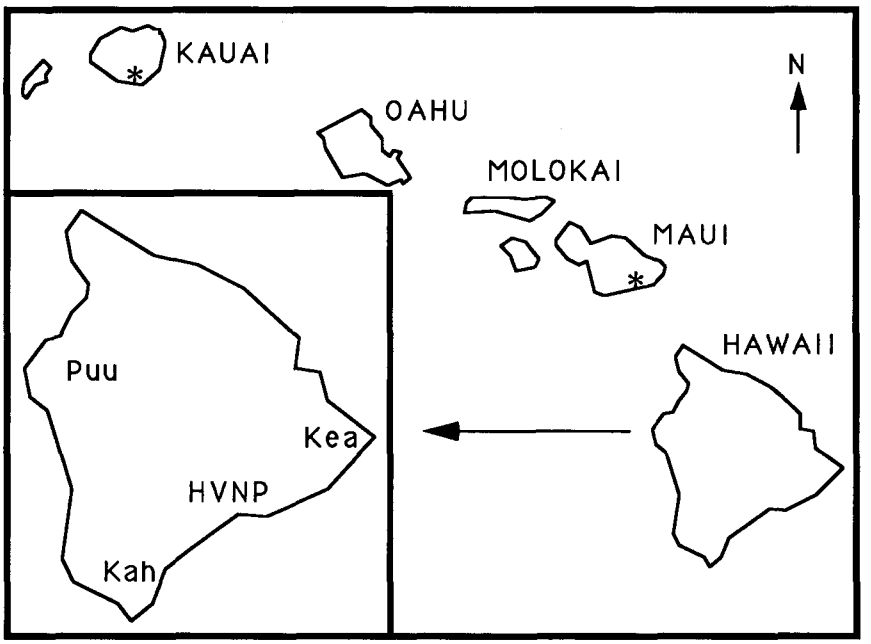

FIGURE 1. Locations of wild populations of Nene on Hawaii (Hawaii Volcanoes National Park [HVNP], Kahuku [Kah], Keaau [Kea], and Puuwaawaa [Puu]), Maui (Haleakala National Park), and Kauai (Waiopili Spring).

population; Black et al. 1991) in 1990 and 1991. Blood samples taken from mated pairs were noted. Methods for preserving blood samples and obtaining DNA fingerprints were the same as those used by Rave (1994). DNA was isolated, digested with restriction endonuclease *Hae*III, electrophoresed in a 1% agarose gel, and vacuum-blotted to a nylon membrane. Molecular size markers were run on each gel, and internal standards (lambda *Hin*dIII) were run within each lane. Every effort was made to equalize DNA concentrations among lanes. Membranes were prehybridized (Westneat et al. 1988) then hybridized sequentially with radioactively labelled M13 bacteriophage DNA (Vassart et al. 1987), Jeffreys' 33.15 and 33.6 human minisatellite DNA (Jeffreys et al. 1985b), and finally with lambda *Hin*dIII to document occasional band shifts. Membranes were washed (Westneat et al. 1988) and exposed to X-ray film to produce autoradiographs of DNA fingerprints.

For each autoradiograph, I calculated similarity coefficients (S; Lynch 1990) between all paired combinations of birds within the same population using the following formula:

$$S = 2N_{AB}/(N_A + N_B),$$

where N_{AB} is the number of fragments shared by individuals A and B, and N_A and N_B are the total number of fragments present for individuals A and B, respectively. All fragments greater than 1.9 kilobase pairs were scored and assumed to be unlinked. For each population, I obtained a similarity coefficient distribution and a mean similarity coefficient by combining the data for all probes.

I used Mantel tests (NTSYS-pc; Rohlf 1990, Schnell et al. 1985) to determine differences in similarity coefficient distributions among the six Nene populations. I also used Mantel tests to determine the presence or absence of random mating by comparing similarity coefficient distributions of mates to the overall distributions of their respective populations. Two matrices consisting of similarity coefficients between all pair-wise combinations of birds and their corresponding site or mating status were compared using the Mantel test statistic Z (NTSYS-pc; Rohlf 1990). Significance among similarity coefficient distributions was determined by comparing t-values, which were calculated from Z-values, with the standard t-distribution (Schnell et al. 1985) and by comparing Z-values with 9,999

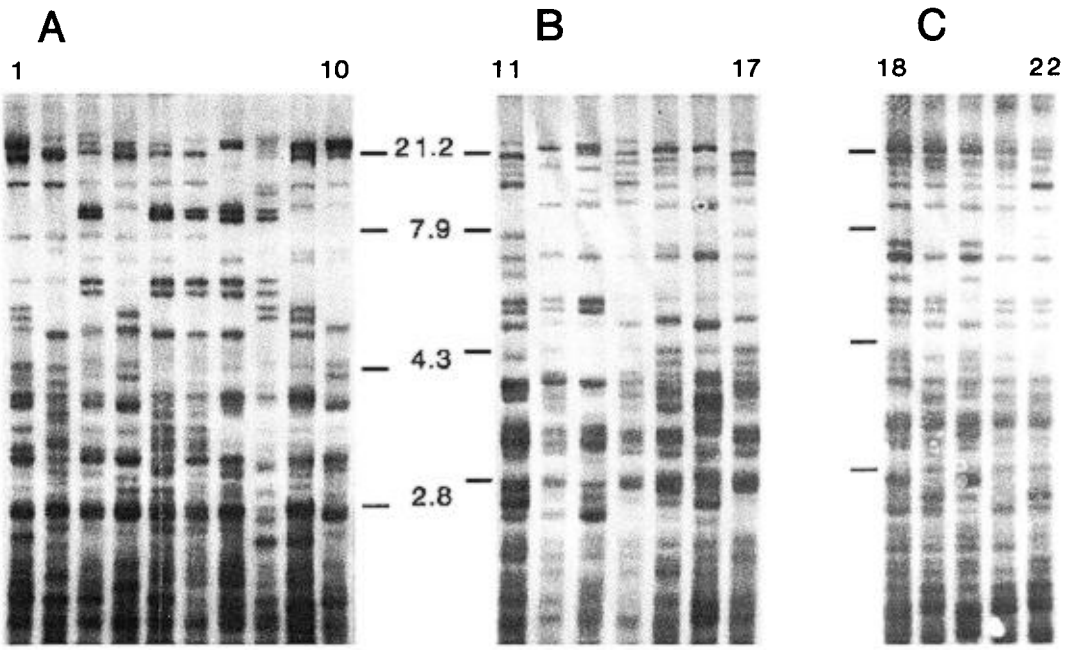

FIGURE 2. DNA fingerprints of wild Nene digested with *Hae*III and probed with (A) Jeffreys' 33.15 and (B and C) M13. Markers are in kilobase pairs. (A) Nene from the Hawaii populations of Keaau (lanes 1–6), Hawaii Volcanoes National Park (lane 7) and Puuwaawaa (lanes 8–10). (B) Nene from Maui. (C) Nene from Kauai.

random samples of their permutational distributions (Rohlf 1990).

For each population, I calculated the band-sharing probability ($\bar{x}$), or the probability that a band present in one individual is found in another (Jeffreys et al. 1985b), using the following formula:

$$\bar{x} = [(N_{AB}/N_A) + (N_{AB}/N_B)]/2.$$

$\bar{x}$ was used to calculate mean allele frequency (q) and mean number of alleles per locus ($1/q$, assuming little variance in q between alleles; Jeffreys et al. 1985b). To assess differentiation among Nene populations, I used Lynch's (1990) estimate of F', which is a modification of Wright's (1951) measure of population subdivision. F', equivalent to F_{st}, equals zero when populations are not different and one when populations are fixed for different alleles (Wright 1951).

To compare genetic differences between wild and captive populations, blood samples from 29 captive Nene at the Olinda Endangered Species Captive Propagation Facility on Maui (formally Pohakuloa, Hawaii) were collected and fingerprinted (Rave et al. 1994). Captive Nene from Slimbridge, England were not used in these analyses because they had no unique fingerprint fragments when compared to Olinda Nene (Rave et al. 1994) and have not been used in captive releases since 1978 (Kear and Berger 1980). I compared the similarity coefficient distribution for all probes combined to distributions of the wild populations, and I assessed population subdivision between captive and wild populations using the same methods as used to compare wild populations (see above). Additionally, a search was made for unique fingerprint fragments in wild birds when compared to captive birds.

RESULTS

DNA fingerprints, similarity coefficient distributions, and mean similarity coefficients revealed low levels of genetic diversity among wild Nene populations (Figs. 2 and 3; Table 1). Although similarity coefficients of Nene from HVNP ranged lower than those from any other area, all populations revealed high degrees of similarity (Fig. 3; Table 1), with many shared DNA fingerprint fragments among populations (Fig. 2). The total number of bands scored for each Nene ranged from 52–81; mean number of

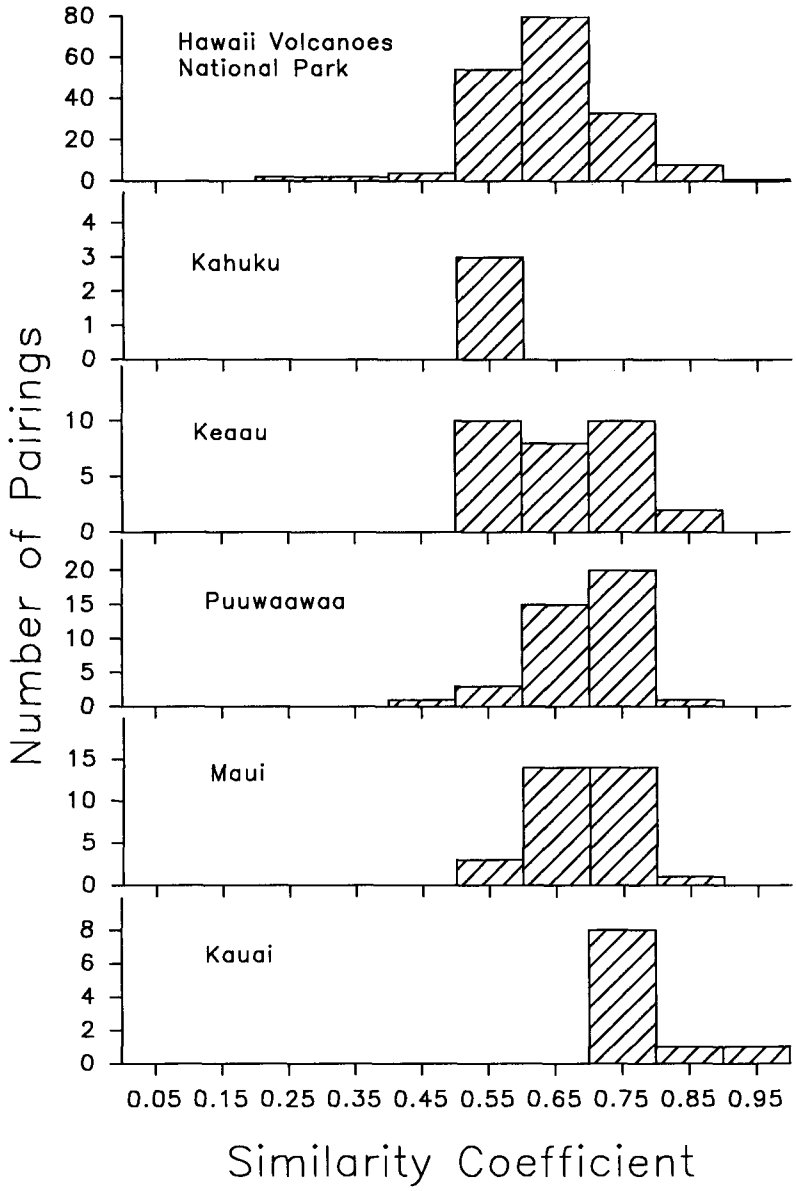

FIGURE 3. Distributions of similarity coefficients for wild populations of Nene on Hawaii (Hawaii Volcanoes National Park, Kahuku, Keaau, and Puuwaawaa), Maui, and Kauai.

bands scored did not differ among sites ($F = 1.07$, $P > 0.05$). No differences were found between similarity coefficient distributions of mated pairs and distributions for their respective populations ($t = 0.08$–1.66, $P > 0.05$), indicating that the degree of relatedness for pairs was not different from random mating expectation.

Nene from HVNP had a significantly lower similarity coefficient distribution than all other wild populations ($t = 2.88$–6.37, $P < 0.05$) except Kahuku ($t = 0.15$, $P > 0.05$; Fig. 3). In contrast, Nene on Kauai had the highest similarity coefficient distribution, significantly higher than all other populations ($t = 2.81$–6.37, $P < 0.05$; Fig. 3). Keaau and Maui had similar distributions ($t = 1.02$, $P > 0.05$), which were both significantly

lower than the distribution from Puuwaawaa (t = 2.42 and 2.44, $P < 0.05$; Fig. 3).

Mean band-sharing probabilities and allele frequencies revealed similar patterns, with Nene from HVNP and Kahuku having the lowest means, Kauai the highest, and Nene from Keaau, Maui, and Puuwaawaa having intermediate means (Table 1). Accordingly, the number of alleles per locus was highest in Nene from HVNP and lowest in Nene on Kauai (Table 1). Differentiation among Nene populations was 0.086 and generally reflected an absence of DNA fingerprint fragments in Nene from Puuwaawaa that were represented in other populations.

The mean similarity coefficient of captive birds at Olinda was 0.666 (Rave et al. 1994). Olinda Nene had a significantly higher similarity coefficient distribution than HVNP Nene (t = 5.18, $P < 0.05$), a significantly lower distribution than Kauai and Puuwaawaa Nene (t = 5.22 and 3.37, respectively, $P < 0.05$) but did not differ from Kahuku, Keaau, and Maui Nene (t = 0.29–1.32, $P > 0.05$). No unique DNA fingerprint fragments were found in any wild birds when compared to captive birds. However, not all fragments present in captive Nene were represented in every wild population. Differentiation between captive and wild populations was 0.088 and generally reflected a paucity of fingerprint fragments in Nene on Kauai when compared to captive birds.

TABLE 1. Comparison of DNA fingerprint analyses of wild populations of Nene on Hawaii, Maui, and Kauai.

	Mean similarity coefficient ($\bar{S}$)	Mean band sharing probability ($\bar{x}$)	Mean allele frequency ($\bar{q}$)	No. of alleles per locus (l/q)
Hawaii				
HVNP	0.634 (184)*	0.640	0.400	2.50
Kahuku	0.640 (3)	0.644	0.403	2.48
Keaau	0.670 (30)	0.672	0.427	2.34
Puuwaawaa	0.702 (40)	0.707	0.458	2.18
Maui	0.679 (32)	0.681	0.435	2.30
Kauai	0.773 (10)	0.775	0.525	1.90

* Number of pairings.

DISCUSSION

Nene within HVNP had the lowest similarity coefficient distribution and, therefore, the highest level of genetic variation among all wild populations. HVNP supports the largest number of birds, yet fewer captive Nene from Pohakuloa/Olinda were released here than in any other Hawaii population except Keaau (Black et al. 1991). Survivorship and recruitment of Nene from different areas are high. Many birds in HVNP are hatched and reared by captive pairs in open-topped pens located within HVNP (Black et al. 1991). Unlike most Olinda birds, whose young often are reared by foster parents, the supplemental captive birds raise their own young. These parent-reared Nene appear to survive better in the wild (Marshall and Black 1992), perhaps contributing to the high survivorship of Nene in HVNP. In addition, much of the suitable lowland habitat for Nene occurs within HVNP, potentially increasing the recruitment of individuals from other populations. Indeed, many Nene from other populations on Hawaii have immigrated to HVNP (J. Black, unpubl. report). If selection is absent, successful colonization of only one migrant into a population per generation can prevent homozygosity from accumulating (Crow and Kimura 1970). Thus, genetic benefits of a large population, such as increased genetic diversity and decreased levels of inbreeding (Wright 1931, Nei et al. 1975), can be achieved even with low migration rates (Foose et al. 1986).

At Kahuku, the low similarity coefficient distribution might not be indicative of the overall population, because sample size was small (i.e., three birds). Further, two of these Nene were captive releases from Pohakuloa/Olinda. Their similarity coefficient was 0.681, a number similar to the mean at Olinda (0.666; Rave et al. 1994). In contrast, the third bird was unbanded, and similarity coefficients between it and the captive releases were lower: 0.610 and 0.627. Larger sample sizes are needed to determine the reliability of Kahuku's similarity coefficients.

Similarity coefficient distributions of Nene at Keaau and on Maui were similar to one another and intermediate in their values, probably because these Nene were derived solely from captive releases. The highest similarity coefficients were found at Puuwaawaa and on Kauai. Unlike other populations, Nene at these sites were captured during late spring and early summer, when flocking of family groups occurs (Elder and Woodside 1958) and when capturing more than one Nene at a time was not unusual. Because all birds were previously unbanded, they were assumed to be unrelated. However, high similarity among birds could suggest that some related individuals (i.e., parent/offspring or siblings) were

inadvertently classified as unrelated in the analyses.

Inbreeding also can contribute to the high similarity found at Puuwaawaa and on Kauai. During the 1960s and 1970s, captive goslings were reared in large groups, regardless of family origin. The lack of defined family groups can prevent correct sibling imprinting among goslings. Additionally, offspring from the same parents were released at the Keauhou II Sanctuary, of which Puuwaawaa is a part, over many years (F. Duvall, pers. comm.). These factors can lead to pair formations of related individuals. On Kauai, 55 Nene were counted in 1991 (Black et al. 1991), prior to the release of captive birds on the island. These Nene descended from the initial flock of 12, which itself was founded by only three breeding pairs (Black and Banko 1994). Because blood samples were obtained prior to captive releases, high similarity of Nene on Kauai likely reflects a small, isolated, inbred population with no immigration. Indeed, several studies have shown increased similarity in DNA fingerprint profiles for animal populations in similar situations (Faulkes et al. 1990; Gilbert et al. 1990, 1991; Reeve et al. 1990; Wayne et al. 1991; Triggs et al. 1991, 1992; Haig et al. 1993).

Mean similarity coefficients and band-sharing probabilities of all wild Nene populations were high when compared to those of other outbred avian species, which typically average less than 0.30 (Burke and Bruford 1987, Wetton et al. 1987, Meng et al. 1990, Westneat 1990, Jones et al. 1991, Oring et al. 1992). Furthermore, these outbred species have lower allele frequencies ($\leq$ 0.154) and higher mean number of alleles per locus ($\geq$ 6.5; Meng et al. 1990, Jones et al. 1991) than Nene. Genetic similarity can increase after a population bottleneck (Gilbert et al. 1991, Wayne et al. 1991, Haig et al. 1993) or with inbreeding (Kuhnlein et al. 1990, Jones et al. 1991, Rave et al. 1994). Nene populations not only have undergone a severe population bottleneck but also have suffered high levels of inbreeding in captivity (Kear and Berger 1980).

Most Nene on Hawaii and all Nene on Maui and Kauai descended from captive releases, yet similarity coefficient distributions of many wild populations differed from Olinda's. These differences could reflect varying levels of inbreeding or fixation by drift. Unlike all other populations, Nene on Maui originated from both Pohakuloa/Olinda and Slimbridge, England releases (Kear and Berger 1980). Although the similarity coefficient distribution on Maui did not differ from Olinda's, it was lower than Slimbridge's (unpubl. data). This probably reflected differences in fingerprint-fragment frequencies between the two captive colonies (unpubl. data). For example, if Nene from Olinda and Slimbridge were fixed for different alleles and if individuals from different colonies mated, then similarity coefficients would decline.

No unique DNA fingerprint fragments were found in wild birds when compared to the Olinda captive flock. This implies that the descendants from the last remaining wild birds on Hawaii in the 1950s perished, that all extant genotypes currently are represented in the captive flock, or that not enough wild birds have been analyzed. Whatever the reason, genetic similarities between wild and captive populations were expected, because over 2,100 captive Nene have been released on the islands since 1960 (Black et al. 1991). Indeed, captive releases on Hawaii and Kauai continue today, further contributing to genetic similarities and generally low differentiation among wild and captive populations.

MANAGEMENT IMPLICATIONS

Most Nene populations on Hawaii are dependent upon captive releases to maintain their numbers (Black et al. 1991, Black and Banko 1994), so a decrease in genetic similarity among captive Nene would benefit the wild populations. The addition of wild-caught birds to the Pohakuloa/Olinda flock throughout the years has been successful in reducing genetic similarity (Rave et al. 1994) and alleviating inbreeding depression (Kear and Berger 1980, Rave 1994). More wild pairs of birds, especially from HVNP, should be added to further reduce similarity among captive Nene. Offspring of these birds then could be released into wild populations.

Population numbers at Keaau and on Kauai have increased dramatically. Lowland habitat, good foraging areas, and few predators have contributed to their success (Black et al. 1991). However, not all DNA fingerprint fragments found in captive Nene are represented in these self-sustaining populations. Therefore, to enhance the long-term evolutionary success of these populations, genetic variation should be increased. In the past, founder contributions among captive-released birds were not equalized. Today, however, managers on Kauai are releasing birds from

all available lineages (Black and Banko 1994). Proper management may help reduce genetic losses due to inbreeding and genetic drift, both of which can influence survival or reproductive success of individuals (Ralls and Ballou 1983, Templeton and Read 1983).

Although no unique DNA fingerprint fragments were found among wild birds, not all populations on Hawaii were sampled. In the 1950s, prior to the first release of captive birds, wild Nene bred within the Keauhou I Sanctuary, and they summered near the Kipuka Ainahou Sanctuary (Elder and Woodside 1958). DNA fingerprints of Nene from these populations are needed to adequately determine the existence of unique alleles. If any are found, these birds could be used in the propagation and release programs to further enhance the genetic diversity of captive and wild Nene.

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