FACTORS INFLUENCING REPRODUCTIVE SUCCESS IN CAPTIVE POPULATIONS OF HAWAIIAN GEESE *BRANTA SANDVICENSIS*

ELIZABETH H RAVE[1,2,3], ROBERT C FLEISCHER[2], FERN DUVALL[4] and JEFFREY M BLACK[5]

[1]Department of Biology, University of North Dakota, Grand Forks, ND 58202, USA
[2]Molecular Genetics Laboratory, National Zoological Park, Smithsonian Institution, Washington, DC 20008, USA
[3]present address: Dept. of Biology, Bemidji State University, Bemidji, MN 56601, USA
[4]Department of Land and Natural Resources, Division of Forestry and Wildlife, 54 S. High St., Room 101, Wailuku, HI 96793, USA
[5]Department of Wildlife, Humbolt State University, Arcata, California 95521-8299, USA

We determined the effects of inbreeding, husbandry, age, and pair bond tenure on reproductive success in captive populations of endangered Hawaiian Geese, or Nene Branta sandvicensis. We found evidence of inbreeding depressions among captive Nene from Hawaii. At the Hawaiian colony, fertility, hatchability, and total survivorship decreased as male inbreeding coefficient increased, and survivorship decreased as co-ancestry coefficient increased. Husbandry, age and pair bond tenure also influenced reproductive success. At the Hawaiian colony, fertility increased with pair bond tenure, hatchability decreased with incubation type, and total survivorship decreased with incubation type and female age. To maximize reproductive success within the colonies, inbreeding should be minimized, older females should not be allowed to breed, and pair bonds should be maintained.

Keywords: Hawaiian Goose, Husbandry, Inbreeding Depression, Nene, Reproductive Success

Many factors can influence reproductive success in captive populations of animals. For example, inbreeding depression, or the reduction in fitness due to effects of inbreeding, is a potential threat to the maintenance of small populations (Senner 1980, Frankel & Soulé 1981, Gilpin & Soulé 1986). Inbreeding reduces individual fitness by decreasing heterozygosity, thereby increasing the expression of deleterious recessive alleles (Frankel & Soulé 1981). Reduced fitness is observed most often in reproductive traits. Indeed, lower fecundity, fertility and survivorship have been documented extensively among inbred laboratory and domestic animals (Lasley 1972, Wright 1977, Falconer 1981) and among inbred populations of captive and wild mammals and birds (Greenwood *et al.* 1978, Ralls *et al.* 1979, van Noordwijk & Scharloo 1981, Ralls & Ballou 1983, Templeton & Read 1983, Laikre & Ryman 1991, Jiménez *et al.* 1994). Although inbreeding depression is not universal (see Gibbs & Grant 1989, Ellegren *et al.* 1993, Worthington Wilmer *et al.* 1993, Ardern & Lambert 1997), it is exhibited by a variety of species and can be particularly problematic for endangered populations. Therefore, determining the presence of inbreeding depression is essential for the proper management of these small populations.

To help increase numbers of the endangered Hawaiian Goose, or Nene *Branta sandvicensis*, captive propagation programmes were initiated in 1949 at the Pohakuloa Endangered Species Facility (now the Olinda Captive Propagation Facility) in Hawaii, and in 1950 at The Wildfowl & Wetlands Trust in Slimbridge, England (Kear &

Berger 1980). Both colonies began with only two geese and one gander (see **Figure 1** for the Pohakuloa/Olinda pedigree). Of these six geese, one was obtained from the wild (c in **Figure 1**), and five were obtained from a privately owned flock (a and b in **Figure 1**), which itself originated in 1918 from only two pairs (Kear & Berger 1980).

Kear & Berger (1980) had evidence that Nene suffered initial inbreeding depressions at both Pohakuloa and Slimbridge. They reported higher fertility at Pohakuloa after three wild birds (d, e, and f in **Figure 1**) were added in 1960 and higher fertility at Slimbridge after four Nene were added, two each in 1962 and 1967. Inbreeding depressions at these colonies, however, were not confirmed statistically.

Additionally, Kear & Berger (1980) suggested that inbreeding may increase the frequency of a deleterious recessive trait that influences gosling survivorship. Goslings normally have a covering of dense down, but some hatch with thin or 'hairy' down. Because hairy goslings lack short down plumules, thermoregulation is inhibited. Consequently, these young are vulnerable at high altitudes in the wild (Kear & Berger 1980).

Other factors including husbandry, age and pair bond tenure can also influence reproductive success. For example, inadequate diet and unreliable incubation techniques lowered fertility and hatchability of Nene during the early years at Pohakuloa. Additionally, age and pair experience influenced reproductive variables such as clutch size, fertility and hatchability at both captive colonies (Kear & Berger 1980). Age (Hamann & Cooke 1987, Hardy & Tacha 1989, Forslund & Larsson 1992, Rockwell *et al.* 1993, Black & Owen 1995) and pair bond tenure (Forslund & Larsson 1991, Black *et al.* 1996) commonly influence reproductive success in other species of geese as well.

Clutch size, fertility, hatchability and survivorship of captive Nene have fluctuated greatly since the colonies began. However, the extent to which inbreeding, husbandry, age or pair bond tenure of Nene have influenced these reproductive variables has not been determined. Therefore, we used multiple regression methods to analyse the effects of pedigree-based estimates of inbreeding, DNA fingerprint-based estimates of inbreeding, husbandry, age and pair bond tenure on measures of reproductive success in Nene at the two captive colonies.

Methods

From the pedigree of Nene at the Pohakuloa/Olinda captive colony (**Figure 1**; hereafter called Olinda), we used a pedigree analysis programme (Genetics; Ballou 1989) to calculate an inbreeding coefficient (F) for each Nene and a co-ancestry coefficient (F_{ij}) between each breeding pair of Nene. The co-ancestry coefficient of a pair equals the inbreeding coefficient of the pair's offspring. Because a complete pedigree of Nene at Slimbridge was unavailable, inbreeding and co-ancestry coefficients of these birds could not be calculated.

Rave *et al.* (1994) found a positive relationship between co-ancestry coefficients obtained from pedigrees and genetic similarity coefficients obtained from DNA fingerprints. Thus, we also determined the effects of genetic similarity on reproductive success by obtaining DNA fingerprints from 24 breeding birds at Olinda and from 44 breeding birds at Slimbridge (Rave *et al.* 1994). Methods for obtaining DNA fingerprints were the same as those used by Rave (1994) and by Rave *et al.* (1994). From the DNA fingerprints, we calculated similarity coefficients (S; Lynch 1990) between breeding pairs of Nene using the formula [1] $S = 2N_{AB}/(N_A + N_B)$, where N_{AB} is the number of fingerprint 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. A higher S value means a greater degree of genetic similarity. Combining the data for three probes produced a weighted mean similarity coefficient for each breeding pair (Rave *et al.* 1994). For each bird, we also averaged the number of fragments among all probes to obtain another measure of genetic diversity (more fragments mean greater diversity).

We summarised husbandry, age, pair bond tenure and reproductive data for 221 breeding Nene at Olinda from 1957-58 to 1991-92 (Nene at Olinda breed from October through April). Data from the 1958-59 and 1970-71

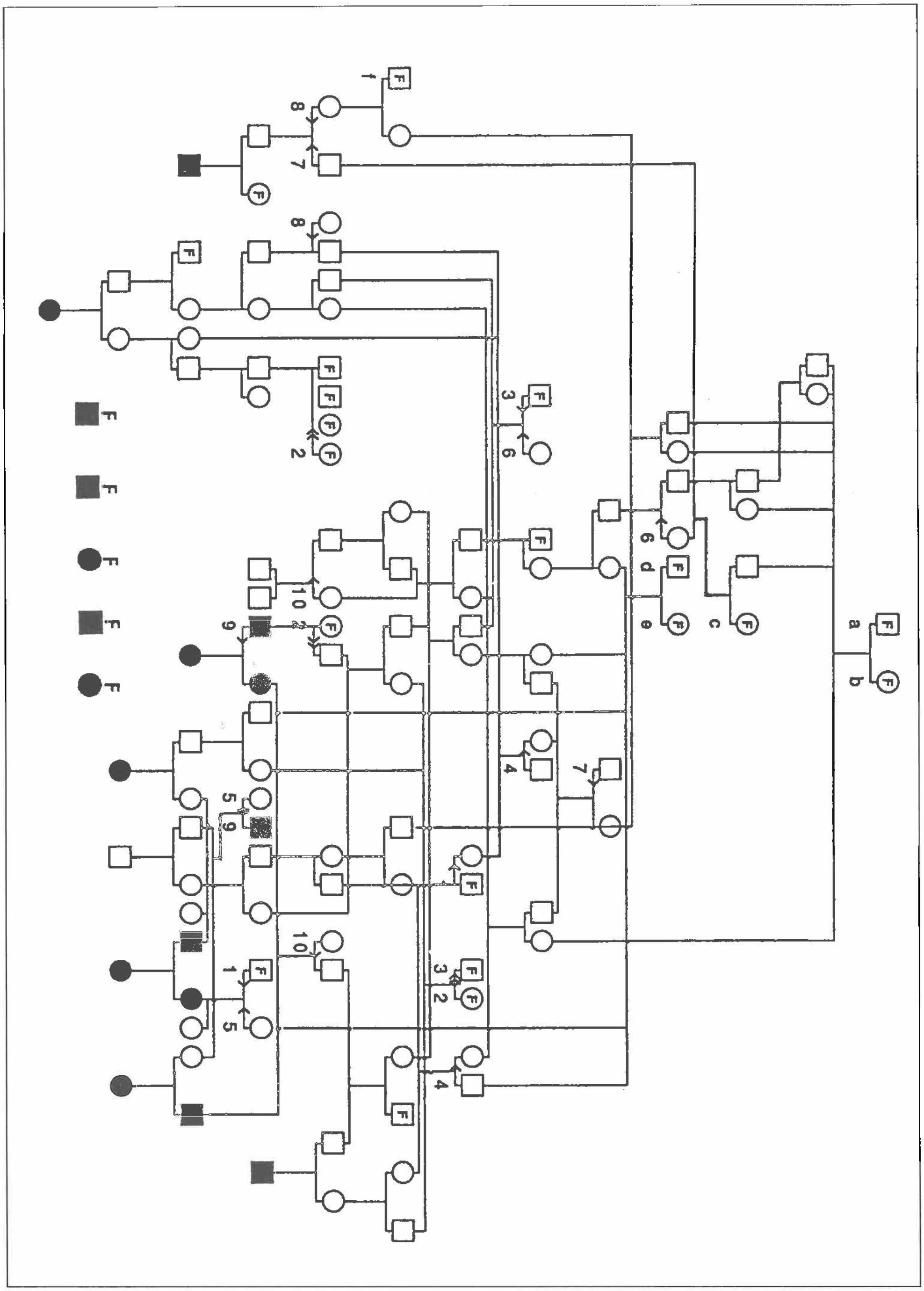

Figure 1. Pedigree of the Pohakuloa/Olinda, Hawaii captive flock of Nene from 1949 to 1992. F = founders, darkened squares (males) and circles (females) are birds in the colony as of 1992, and arrows represent those individuals found elsewhere within the pedigree.

breeding seasons were unavailable. We also summarised data for 44 breeding Nene at Slimbridge from 1990 to 1992 (Nene at Slimbridge breed from February through April).

For each clutch laid per pair of Nene during each breeding season at Olinda, we recorded (1) type of egg incubation (*ie* by the goose herself, by a foster bird of the same or different species, or in an incubator; dummy variables 1, 2 and 3, respectively), (2) male and female age (number of years males and females had been in residence at the colony; true ages of the birds were not always known), and (3) pair bond tenure (number of years a male and female had been paired). Of these data, only male and female ages were available for Nene at Slimbridge. We also recorded the number of hairy down goslings hatched at Olinda. Although this trait seems to be genetic (Kear & Berger 1980), no conclusive evidence exists to dismiss a congenital origin.

To measure reproductive success, we recorded the following variables for each clutch laid per pair of Nene during each breeding season at both colonies: (1) number of eggs laid per clutch, (2) percent fertility (number of fertile eggs/number of eggs in clutch), (3) percent hatchability (number of hatched young/number of fertile eggs), (4) percent survivorship (number of fledged young/number of hatched young), and (5) percent total survivorship (number of fledged young/number of eggs in clutch). Percentages were arcsine transformed prior to analyses (Steel & Torrie 1980).

We used stepwise multiple regressions (Sokal & Rohlf 1981) to determine the effects of inbreeding, husbandry, age and pair bond tenure on reproductive success in Nene from both captive flocks. Additionally, the year in which a breeding event occurred and order in which a clutch was laid per breeding season (hereafter called clutch number; Nene typically lay several clutches during one breeding season) were used as covariates. We used each clutch laid throughout the duration of the study as an independent data point (see Daniell & Murray 1986, Brewer *et al.* 1990). However, because many of the same pairs and individuals in new pairs bred across years, non-independence resulted. Thus, we also averaged the data from each breeding pair across all years to obtain single means for each pair (see Greenwood *et al.* 1978, Gibbs & Grant 1989). We then compared the results of the two analyses to ascertain support for each effect. We placed greater reliability in those results that were significant in both regression analyses.

For the Olinda data set, we regressed each of the five reproductive success variables (clutch size, % fertility, % hatchability, % survivorship and % total survivorship) and the proportion of hairy down goslings on the predictor variables (male and female inbreeding coefficient, co-ancestry coefficient of a pair, year, clutch number, incubation type, male and female age, and pair bond tenure). Important interactions among the predictor variables, based on results of a correlation matrix, were also included. Multiple regression models were as follows:

[2] clutch size = constant + year + clutch no.+ ♀ F + ♀ age + pair bond tenure + (year x ♀ F) + (year x ♀ age) + (year x pair bond tenure)

and

[3] % fertility, % hatchability, % survivorship, % total survivorship, or proportion of hairy down goslings = constant + year + clutch no. + ♂ F + ♀F + F_{ij} + incubation type + ♂ age + ♀ age + pair bond tenure + (year x ♂ F) + (year x ♀ F) + (year x F_{ij}) + (year x incubation type).

For those Olinda Nene whose DNA fingerprints were obtained (*ie* Nene in the colony from 1983-1992), the similarity coefficient of a pair and average male and female fingerprint fragment number were used as additional predictor variables. For the Slimbridge data set, we regressed each of the reproductive success variables on the similarity coefficient of a pair, average male and female fingerprint fragment number, year, clutch number, and male and female age.

Results

Inbreeding coefficients of individual Nene and co-ancestry coefficients between pairs of Nene at Olinda both ranged from 0 to 0.250. Similarity coefficients ranged from 0.364 to 0.824, and average number of fingerprint fragments ranged from 16 to 27. At Slimbridge, similarity coefficients ranged from 0.586 to 0.908, and average number of fingerprint fragments ranged from 16.3 to 27.

Significant results of the two regression analyses (using each clutch laid throughout the study as an independent data point, and using the average of each breeding pair across all years) for captive Nene at Olinda from 1957-1992 are shown in **Table 1**. In both analyses, clutch size decreased with year and increased with clutch number, fertility increased with pair bond tenure, hatchability decreased with incubation type, and total survivorship decreased with incubation type and with female age (**Table 1**). Inbreeding and co-ancestry coefficients also affected reproductive success, but the results were significant in only one of the two regression analyses. For example, fertility, hatchability, and total survivorship decreased as male inbreeding coefficient increased, survivorship decreased as co-ancestry coefficient increased, and proportion of hairy down goslings increased as male inbreeding coefficient and co-ancestry coefficient increased (**Table 1**). No interactions among predictor variables were significant when the regression models were run to completion.

For those Olinda Nene whose DNA fingerprints were obtained, we found no evidence that degree of genetic similarity, as measured by similarity coefficient of a pair and average number of DNA fingerprint fragments for each bird, influenced reproductive success.

At Slimbridge, because only three years were included in the study, too few data were available to average variables from each breeding pair across all years. Thus, we were only able to analyse the data using each clutch laid throughout the duration of the study as an independent data point. As the average number of female DNA fragments increased, fertility (r = -0.082, P = 0.033) and total egg survivorship (r = -0.049, P = 0.010) decreased. As the average number of male DNA fragments increased, hatchability (r = -0.142, P = 0.015) decreased. Additionally, hatchability significantly improved throughout the three years (r = 0.292, P = 0.028). Similarity coefficient, clutch number, and male and female age did not significantly influence any measure of reproductive success.

Discussion

This study provides evidence that Nene from Olinda, but not from Slimbridge, suffer adverse consequences from inbreeding. However, because we place greater reliability in those results that were significant in both regression analyses, this study also provides evidence that husbandry, age and pair bond tenure influence Nene reproductive success to a greater degree than does inbreeding. For example, clutch size declined by 1.3 eggs throughout the 35 years for which we had data. Early in the propagation effort at Olinda, productive pairs were encouraged to breed, regardless of their relatedness (Kear & Berger 1980). Thus, many offspring from few parents were being produced and subsequently released in the wild. During the 1980s, however, this practice was restricted. Those Nene whose genes were under-represented in the colony were then encouraged to breed. Consequently, clutch size was not always maximised.

Type of incubation (by the goose herself, by a foster bird of the same or different species, or in an incubator) influenced hatchability and total survivorship of Nene at Olinda. Eggs incubated by their biological mothers had the highest hatchability and gosling survivorship. Eggs incubated by foster birds had moderate reproductive success. Efforts to incubate eggs under these conditions are generally unsatisfactory, because many foster birds fail to become broody during the appropriate time (Kear & Berger 1980). Eggs from incubators had the lowest hatchability and gosling survivorship. 'Problem' eggs (eg those that lost too much water, were soiled, or had hairline fractures) were always placed in an incubator.

Table 1. Results, listed in order of significance, of regression analyses for factors influencing reproductive success in captive Nene at Olinda, Hawaii from 1957 - 1992. For each reproductive variable, 1 = using each clutch laid throughout the study as an independent data point, and 2 = using the average of each breeding pair across all years. *F* = inbreeding coefficient; *Fij* = co-ancestry coefficient; R^2 = proportion of variation accounted for by model; N = sample size.

Reproductive Variable	Regression Coefficients of Predictor Variables
Clutch size	1: year (-0.028***), clutch no. (0.215***), pair bond tenure (0.061***), R^2(0.101), N(855) 2: clutch no. (1.217***), year (-0.029**), R^2 (0.440), N(68)
% Fertility	1: pair bond tenure (0.040**), ♂*F* (-1.023**), ♀Age (-0.017*), R^2 (0.036), N (524) 2: pair bond tenure (0.066*), R^2 (0.063), N (67)
%Hatchability	1: incubation type (-0.288***), ♂Age (-0.030***), ♂*F* (-1.515***), ♀Age (-0.026**), clutch no.(-0.100**), pair bond tenure (0.033*), R^2 (0.158), N (526) 2: incubation type (-0.268**), R^2 (0.160), N (68)
%Survivorship	1: incubation type (-0.121**), R^2 (0.016), N (645) 2: *Fij* (-1.415*), R^2 (0.148), N (60)
% Total Survivorship	1: incubation type (-0.288***), ♂*F* (-1.204**), ♂Age (-0.018**), clutch no. (-0.085*), ♀Age (-0.014*), R^2 (0.133), N (526) 2: incubation type (-0.241***), ♀Age (-0.016*), R^2 (0.210), N (68)
Hairy Down	1: *Fij* (0.441**), ♂*F* (0.346**), year (-0.002*), R^2 (0.070), N (380)

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Additionally, throughout the 1980s, the incubator not only had mechanical problems but was housed in an uncontrolled environment. Thus, not surprisingly, these eggs suffered lower reproductive success.

Female age and pair bond tenure also influenced reproductive success. Younger female Nene reared goslings that were better able to survive to fledging than very old Nene (10+ years), a result also seen in other species of geese (Rockwell *et al.* 1993, Black & Owen 1995). Additionally, more tenured pairs had higher fertility. Nene are one of many avian species that have a long-term monogamous mating system. Among these species, reproductive success commonly improves with increased pair bond tenure (Black 1996).

Inbreeding, especially among males at Olinda, also influenced Nene reproductive success, though to a lesser degree than did husbandry, age and pair bond tenure, since inbreeding results were not shared between the two regression analyses (see **Table 1**). For example, fertility, hatchability and total survivorship declined as male inbreeding increased. Although sperm were never analysed at Olinda, some male Nene had deformed or few sperm during the initial years at Slimbridge (Kear & Berger 1980). However, after two partially wild, and presumably less inbred, male Nene were added to the Slimbridge colony in 1962, egg fertility increased (Kear & Berger 1980). Similar increases in fertility were seen at Olinda after wild males were added in 1960 (Kear & Berger 1980). This suggests that high male inbreeding, with an associated low sperm quality, was responsible for low fertility within the colonies. Although inbred females of other bird species have lower reproductive success (Sittmann *et al.* 1966, van Noordwijk & Scharloo 1981), we found no evidence of this among inbred female Nene.

In contrast, genetic similarity and fingerprint fragment numbers obtained from DNA fingerprint data showed no effect on reproductive success of Nene at Olinda. However, Nene with fewer DNA fingerprint fragments (and thus higher homozygosity) had higher reproductive success at Slimbridge. Many years of inbreeding within the Slimbridge population, which was founded by only seven geese (Kear & Berger 1980), may have purged deleterious alleles. Consequently, Slimbridge Nene seem to tolerate inbreeding better than Olinda Nene. Although high genetic diversity may increase population vigour and the potential for future evolutionary adaptation (Frankel & Soulé 1981), low diversity does not necessarily preclude moderate or high levels of reproductive success (Ellegren *et al.* 1993, Worthington Wilmer *et al.* 1993, Ardern & Lambert 1997). Indeed, in wild Nene populations, the lowest genetic diversity is found in birds on the island of Kauai, where population numbers have increased dramatically (Rave 1995). Although genetic similarity coefficients increase with co-ancestry coefficients (Rave *et al.* 1994), perhaps DNA fingerprint data alone cannot adequately determine the presence of inbreeding depressions. However, fingerprint data can be used to determine degree of genetic diversity between potential mates, which can prove useful in captive propagation programmes (Rave *et al.* 1994).

As male and gosling inbreeding coefficients increased, the proportion of goslings showing the hairy down trait also increased at Olinda. Because husbandry, age, or pair bond tenure did not influence the presence of this trait, there is no evidence from our study that hairy down is congenital. Although some hairy goslings in captivity are at no disadvantage because of adequate heat, others appear sickly and weak (Kear & Berger 1980). Consequently, many birds showing this trait have been culled, especially from the Olinda colony. However, the hairy plumage may represent an adaptation to lower elevations (Kear & Berger 1980). If so, this trait should be retained, but not at the expense of increased inbreeding.

The susceptibility of Nene to inbreeding depression creates a need to minimise inbreeding. Adding wild Nene increased productivity within both captive colonies early in the propagation effort (Kear & Berger 1980). This practice should continue, especially at Olinda, from which Nene are still released yearly into the wild. In addition, co-ancestry and similarity coefficients could be used to determine optimal pairings between males and females that would minimise inbreeding within the captive flocks (Rave *et al.* 1994).

Husbandry, age and pair bond tenure must also be considered when breeding Nene in captivity. Eggs should be kept with their parents whenever possible. This would improve reproductive success and facilitate the learning of behavioural traits by goslings from their parents (Marshall & Black 1992). Females should not be bred in captivity for an extended time, as females bred past age 15 have never produced viable young. Finally, although reproductive success can be enhanced by keeping more tenured pairs together, individuals may need to be periodically remated to reduce inbreeding or to decrease over-representation of genes within the colony. Thus, by reducing levels of inbreeding and by carefully monitoring husbandry, age and pair bond tenure of Nene, reproductive success among captive birds can be improved.

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