

The effect of rearing experience on subsequent behavioural traits in Hawaiian Geese *Branta sandvicensis*: implications for the recovery programme

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Summary

The risk of the Nene *Branta sandvicensis* becoming extinct has been minimized by the release of over 2,000 captive-reared geese, but the population (now at 500) is yet to achieve a self-sustaining status. The majority of birds released have been reared in gosling-only groups, thus missing out on the opportunity to learn social and feeding skills from adults. In this paper we test the hypothesis that rearing experience affects the subsequent behavioural traits of Nene goslings. We raised 42 goslings under four conditions: a gosling group not exposed to adults, a gosling group exposed to adults from 16 days onward, three groups in view of "foster" adults for 14 days, and four groups reared continuously by parents. All birds were eventually released into an 8 ha pen where a flock of adult Nene roamed. The method by which Nene goslings were raised had a significant effect on dominance, flock integration, and vigilance. Parent-reared birds were dominant to and more vigilant than goslings raised without parents or goslings reared in sight of adults. Parent-reared birds also integrated into the adult flock sooner than other goslings. Growth rate and final body size were not affected by rearing regime (with or without parents or foster parents). In future, managers should provide goslings with as much "parental" experience as possible in order to equip them with appropriate skills to cope once released in the wild.

Introduction

The Hawaiian Goose *Branta sandvicensis*, locally known by its Hawaiian name, Nene, was declared by naturalists to be in danger of extinction as early as 1864. Estimates of the population before the European discovery of the islands by James Cook in 1778 are as high as 25,000 (Baldwin 1945, Kear and Berger 1980). By 1950, as few as 17 to 30 birds were estimated in the wild (Smith 1952, Elder and Woodside 1958). In 1949 a recovery programme was initiated by the Hawaiian Division of Fish and Game (now Division of Forestry and Wildlife) and included supporting efforts by Sir Peter Scott at The Wildfowl Trust (now Wildfowl and Wetlands Trust) (Berger 1978, Kear and Berger 1980). In 1958, the first Nene sanctuary was created and in 1960 the first captive Nene were released (Berger 1978). This project, which is now a multi-agency collaborative venture, is ongoing and 2,127 Nene have been released in various areas across the state of Hawaii between 1960 and 1990 (Black *et al.* 1991). Several features of the recovery programme are currently under investigation in order to identify further the limiting factors that influence the low survival and recruitment rates in the wild population (Stone *et al.* 1983, Morin and Walker 1986, Banko 1988, Black 1990).

Although the risk of extinction has been minimized by these efforts, the wild population has not become self-sustaining and in fact is dependent on captive releases to maintain its numbers (Devick 1981a,b, Morin and Walker 1986, Banko 1988, Black *et al.* 1991).

In this paper we explore the possibility that captive-reared Nene are unable to integrate and adjust adequately to the wild environment because of their limited early experiences in captivity. One well-known example of "missing" behaviour traits in a captive-reared endangered species is that of the golden lion tamarin *Leontopithecus rosalia*. In this case, animals involved in initial releases were unable to recognize natural foods or to cope with jungle vegetation, having never had to find food or climb varying obstacles in captivity. Currently, the monkeys to be released are trained in pens that offer changing and challenging obstacles that could improve locomotor ability, spatial orientation and decision-making (Beck *et al.* 1988, Kleiman 1989). Captive-reared Nene could well be subject to "missing" behaviour because the majority have been reared without parents.

Young geese are thought to learn important social and foraging skills from their parents. For example, full-grown Barnacle Goose *Branta leucopsis* goslings reared in captivity without parents scored lower in dominance interactions with parent-reared goslings when released in a gosling-only situation (Black and Owen 1987). Orphaned goslings (which has been the status of many released captive-reared Nene) are attacked more frequently, feed almost continually and achieve a poorer body condition than those in families (Black and Owen 1984, 1989a,b).

The survivability of Nene from the initial releases was only 48% by the birds' second year of life (N. Santos in Banko and Elder 1989). Those that survived had smaller clutches and were less likely to breed than unbanded (presumed wild) Nene (Devick 1981b). The majority of these geese were reared at the original Hawaiian breeding centre, Pohakuloa, where they were removed from parents soon after hatching and reared in large groups. Similarly, those reared at Slimbridge and later released on Maui were hatched in incubators and reared in large groups without parents (Kear and Berger 1980).

In the later years of the programme different styles of rearing have been employed. At the current Hawaiian breeding centre, Olinda, goslings are placed in broods that have visual and vocal contact with a pair of adult Nene for the first 14 days after hatching, a system based on potential problems with disease and imprinting on food (kikuya grass) and the hope that goslings will imprint on adults and learn adaptive behaviours (Gassmann-Duvall 1987, Black 1990). At other areas in the national parks and state sanctuaries goslings have been parent-reared in open-topped pens from which the young are allowed to fly.

In this study we reared Nene goslings in a similar range of regimes and after their release onto the Slimbridge grounds we assessed their relative ranks in social skills, predator response, flock integration and growth rates. Based on similar projects with goslings of captive Canada Geese *Branta canadensis* (Black and Barrow 1985) and Barnacle Geese (Black and Owen 1987) we predicted that: (1) goslings reared in sight of "foster" adults would be similar in size but dominant over goslings not exposed to adults; (2) parent-reared goslings would be similar in size but more dominant and socially adept than those reared in

view of "foster" adults; and (3) the goslings' final rank in terms of potentially adaptive behaviours would be in the order of (a) parent-reared, (b) long-term foster-reared, (c) short-term foster-reared and (d) not parent-reared.

Methods

In 1990 Nene goslings were raised in four rearing regimes at The Wildfowl and Wetlands Trust (WWT), Slimbridge, United Kingdom, as follows: LTFR = long-term foster-reared: sibling group in view of an adult pair of Nene beginning at 16–30 days after hatching (12 birds in one large group); NPR = not parent-reared: sibling group not exposed to adult Nene (11 birds in one large group); STFR = short-term foster-reared: three groups in view of a pair of foster adults for their first 14 days after hatching, as at Olinda, Hawaii (nine birds in groups of two, three, and four); PR = parent-reared: four groups reared by parents on the WWT grounds (10 birds in groups of two, two, three, and three). Because of the disparity of the goslings' ages, initial interactive tests were limited to two sets of groups, the two larger groups (LTFR vs. NPR; hatched 19 March–2 April 1990) and the two smaller groups (STFR vs. PR; hatched 18–29 April 1990, with the exception of one PR group that hatched 30 March 1990). In addition, the majority of goslings in LTFR and NPR groups were from first-clutch eggs and those from STFR and PR were mostly from second-clutch eggs. Brood sizes in the wild range from one to five or six goslings.

Rearing situations

We reared the LTFR and NPR groups in outdoor pens (30 × 15 m) with a pool and at night in a heated shelter (until fully feathered). When LTFR goslings were between 16 and 30 days of age (17 April 1990) we placed a pair of adults (FH/FI, paired for one year) in the neighbouring pen with two wooden panels removed and replaced with screen mesh. The goslings and adults could thus interact through the wire mesh. We removed the adults four months later (17 August 1990) and goslings (138–152 days old) were transferred to a new set of grass "observation" pens (30 × 15 m) where we recorded behaviour and interactive encounters within groups.

The STFR groups were reared in covered brooders (1.5 × 0.5 m) with heat lamps and a larger space for exercise. This design allowed the goslings to be in view of a pair of adults (BU/BV, paired for three years), to have access to grass, and to be kept warm at night. We positioned the brooders so the groups could not see each other as at the Olinda breeding centre. Each brood was screened from view of the adults at age 14 days, and the adults were removed after all broods reached 14 days. After we removed the foster parents and when the goslings were fully feathered, the separate groups were kept in fresh grass pens (5 × 7 m) with free access to shelters. This regime continued until they were 135–141 days old when we moved them into the "observation" pens, as above.

The PR goslings roamed the grass lawns and lakes of the Big Pen (8 ha) except one family which lived in a smaller area (100 m²) with a pool and running water. A flock of 90 adult Nene and numerous other waterfowl species also roamed the Big Pen. When they were 130–137 days old (except the oldest brood, 160 days

old) the parents were removed (5 September 1990) and we transferred the goslings to "observation" pens, as above.

The rearing regime for PR goslings differed from the others in that they got more exercise in the large pen, encountered other Nene and other species of waterfowl and, although plentiful, their food source was not available on an ad lib basis. To check what effect these differences had on PR gosling growth rates, in 1991 we reared two additional families (three goslings each with their parents) in the same area and feeding regime as the LTFR, NPR and STFR groups.

In accordance with British law all goslings were made flightless. The operation was performed around age five days when minimal harm was done. On 16 April 1990 all goslings were wormed with Ovitelmin and on 7–10 June 1990 all birds were treated for parasites with a subcutaneous injection of Ivermectin.

Dominance assessment

We determined the social rank order in each group by behaviour sampling (Martin and Bateson 1986) during observation sessions lasting between 10 minutes and one hour. During the sessions we recorded the number and direction of displacements/supplants, pecks, chases, social greetings and facing away, all of which reflect social rank order among the participants (Radesater 1974, Black and Owen 1987). Physical contact was rare and injuries did not occur. Linear rank order was established by the proportion of encounters won by each gosling arranged in a matrix so that the least number of circularities occurred. Within-group ranks were assessed when LTFR and NPR goslings were 96–175 days old and STFR and PR goslings were 122–173 days (the oldest brood was 152–192 days).

To assess the outcome of interactions between groups, we transferred a set of goslings from each group into a new grass pen (10 m²) where a social rank order developed through greeting postures or aggressive threats (as above). The LTFR vs. NPR sets included the three top-ranked birds, the second three, third three and the bottom-ranked birds (three from LTFR and two from NPR). The STFR vs. PR sets included the top three, the middle four and the bottom-ranked birds (two from STFR and three from PR). The outcomes of encounters were arranged in a matrix so the least number of circularities occurred, as above. LTFR and NPR goslings were 173–210 days old and STFR and PR goslings were 180–205 days (the oldest brood was 210–224 days).

In order to assess the relative dominance between all four rearing regimes in January 1991 we grouped the most dominant gosling from each group in the observation pen, then the second most dominant bird from each group, then the third, then the fourth. This time, however, we grouped only same-sexed birds, since males were larger than females. The age in days of these goslings was 295–363 (LTFR and NPR) and 268–333 (STFR and PR; the oldest two were 298–352) at this time and the birds had already experienced up to 295 (LTFR and NPR) and 286 (STFR and PR excluding the oldest PR group, which was in a separate pen most of the time) days respectively in the Big Pen where they interacted with the adult Nene flock.

Release

Goslings were between 196 and 227 days of age when they were released into the Big Pen area. At this stage their plumage was similar to adult plumage. The parents of the PR goslings were temporarily removed from the adult Nene flock before the release, and for the duration of the study.

During the first week after release, we observed goslings for two consecutive days during two-hour periods spaced throughout the daylight hours. We recorded their location, nearest neighbour, and agonistic encounters. We attempted to locate all birds every 15 minutes during the two-hour session. This task was made easier in LTFR and NPR goslings because they stayed in large flocks during the first weeks. Many of the STFR and PR goslings split up immediately after release, so we located each small flock or single bird at least once during the observation period.

In the eighth week after the release we repeated the observations after the goslings had become more accustomed to the situation. We attempted to locate each bird five times during a two-day period and watch individuals for a period of 10 minutes each. The nearest gosling and adult neighbour were recorded at the start and end of each session.

Vigilance

We monitored each groups' immediate reaction and subsequent vigilant behaviour by walking a black labrador retriever along a side of the observation pen; feral dogs are one of the major predators of released Nene in Hawaii. These pens were screened so that only one group could see the dog at a time. We recorded whether the birds approached, hissed at or grouped together and were decoyed (followed the predator) by the dog. Beginning five minutes after the predator was out of sight, we recorded the number of heads up (HU) each minute for an hour. The number of heads up in a flock normally declines steadily during 30 minutes after a predator introduction (Madsen *et al.* 1989, Black and Burn unpublished data). Data were taken from two predator introductions.

Growth

We measured the goslings on Mondays and Thursdays for the first 63–70 days after hatching, then on Mondays to ages 127–141 days with the exception of PR goslings. PR goslings were measured only on Mondays to minimize the stress of frequent captures in the Big Pen. We measured their weight, skull (bill and head) and tarsus. We also measured them on the day of their release into the Big Pen.

The growth coefficients were calculated for each gosling based on the Gompertz equation:

$$M(t) = A \{ 1 + \exp[-K(t - I)] \}^{-1}$$

to estimate K , the growth rate constant, A , the asymptotic size, and I , the age in days at inflection (the increase in the growth curve) (Ricklefs 1984, Ricklefs *et al.*

1986, Boag 1987). Two-way ANOVA was used to examine the effects of rearing regime (group) and sex on growth rates.

We measured the two families of 1991 PR goslings three times. We compared these measurements with those from the 1990 PR goslings that were reared in the free-range situation in the Big Pen.

Results

Social ranks/dominance

Initially, LTFR goslings won more and lost fewer interactions when encountering NPR goslings ($X^2 = 16.0$, $df = 2$ wins, losses and ties, $P < 0.001$), whereas the number of wins, losses and ties was similar in encounters between STFR and PR goslings ($X^2 = 4.3$, $df = 2$, $P > 0.1$).

At the later age, when interactions were between a gosling from each group but were limited to one sex within a trial, dominance rank was ordered, from winners to losers: PR, STFR, NPR and LTFR ($r^s = -0.509$, $P < 0.005$, $N = 28$) (see Figure 1).

Initial rank order within groups was positively correlated with size and sex (males are larger than females) in all but the PR group (Spearman, see Table 1). Three females in the PR group were initially dominant over all the other PR birds. However, the ranks changed after the first dominance assessment and the females became subordinate to the PR males.

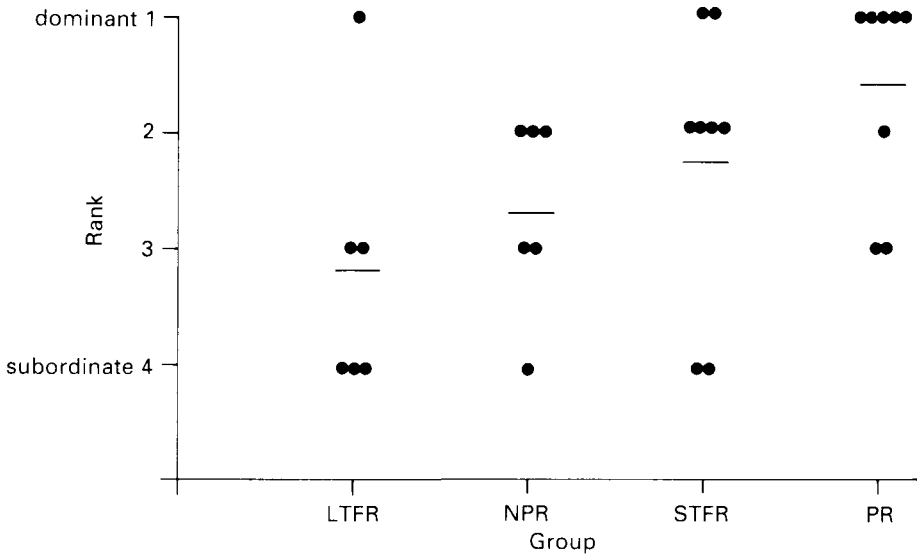


Figure 1. The frequency of dominance rankings for goslings reared under different situations. Up to four goslings of the same sex (one from each regime) were assessed together. LTFR, long-term foster-reared goslings; NPR, goslings not parent-reared; STFR short-term foster-reared goslings; PR parent-reared goslings. Bars represent the mean rank for each group.

Table 1. Spearman rank correlations between social rank, sex and size within each of the four rearing regimes

	Sex	Weight	Skull	Tarsus	Wing
Rank					
LTFR	0.648*	NS	NS	-0.650*	NS
NPR	-0.671*	-0.635*	-0.733*	NS	NS
STFR	-0.866*	NS	-0.867**	-0.750*	-0.857**
PR	NS	NS	NS	NS	NS
Sex					
LTFR		NS	0.518*	0.518*	0.649*
NPR		0.674*	0.672*	0.596*	0.671*
STFR		0.696*	0.866**	0.779*	0.837*
PR		NS	0.873**	NS	NS

*Significant at the 0.05 level; **significant at the 0.01 level.

LTFR, Long-term foster-reared; NPR, not parent-reared; STFR, short-term foster-reared; PR, parent-reared.

Simulated release

In the first week after release, goslings from all four rearing regimes were recorded almost entirely with other goslings; there was no difference between groups ($KW = 1.34, df = 3, P = 0.719$) (Figure 2). By the eighth week, however, a significant degree of variation in nearest-neighbour associations was detected

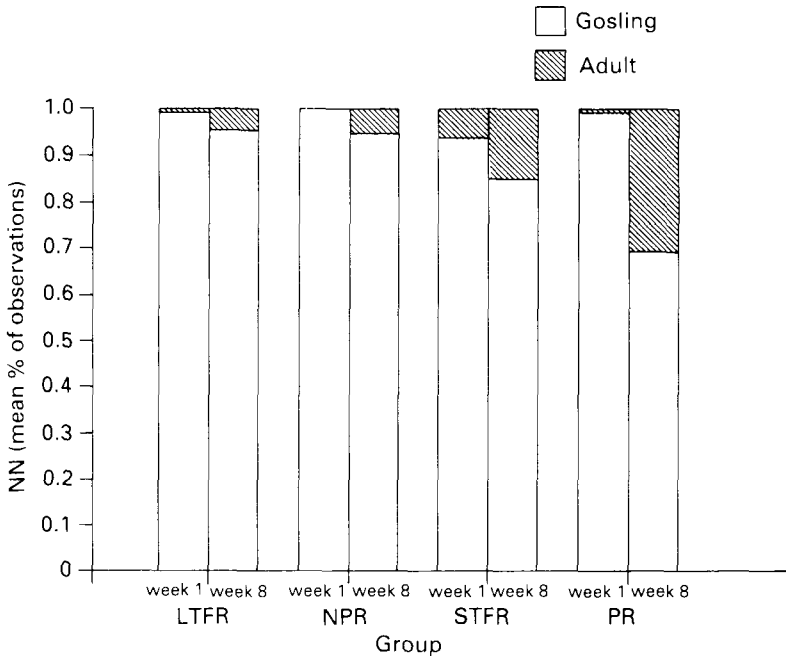


Figure 2. The proportion of nearest-neighbour records (nearest to goslings or adults) for goslings from different rearing regimes one week and eight weeks after release into an area where adult Nene roamed. See Figure 1 for explanation of headings.

between groups ($KW = 7.82$, $df = 3$, $P = 0.05$). The difference was most evident in PR goslings who spent an increasing amount of time with adult flock members and less with other goslings (Figure 2).

The two PR goslings that were reared apart from other birds (in a separate pen: see Methods) ranked intermediately among other PR goslings in the adult/gosling associations. This suggests that early experience in the Big Pen for the majority of the PR goslings may not have caused the difference in associations in Figure 2.

Vigilance/predator response

The initial reaction to the potential predator was similar in LTFR, NPR, STFR groups. At least one and up to three goslings in these groups ran towards the predator (coming within 2 m) for brief periods of displaying the low neck threat posture while hissing. Others called loudly and followed in mass as near as 5 m, being decoyed (followed the predator) by the dog. Goslings in the PR group, on the other hand, kept their distance (staying at least 8–10 m away). Members of this group gathered together in a tighter mass than the other groups and they were not decoyed. Their vocalizations were less loud than in the other groups.

The PR goslings were most vigilant during the period following their experience of a predator (Figure 3). Analysis of variance revealed significant differences between the rearing regimes ($F = 13.4$, $df = 3$, $P = 0.005$) and the periods before and after the predator introductions ($F = 5.3$, $df = 2$, $P = 0.048$). The PR group also remained vigilant for the longest period after the predator

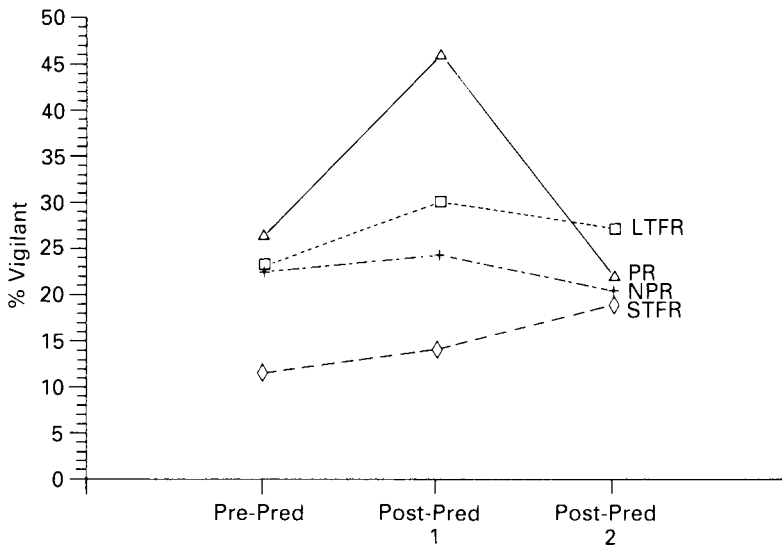


Figure 3. The percentage of goslings from the four rearing regimes that were vigilant (with heads up) before and after the presentation of a mock predator. Pre-Pred = 30 minutes before the predator was introduced, Post-Pred 1 = first 30 minutes following introduction of the predator, Post-Pred 2 = second 30 minutes after the predator was introduced.

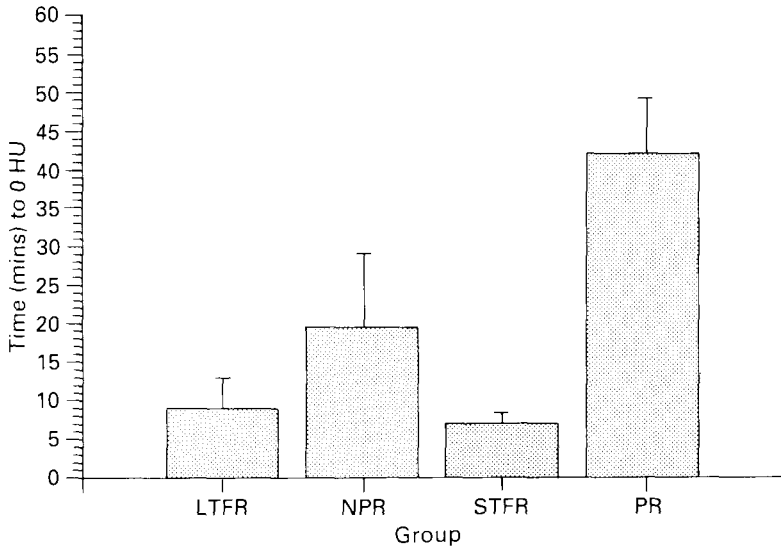


Figure 4. Duration of vigilance postures (time to zero heads up (HU)) after the presentation of a mock predator for goslings with different rearing regimes. See Figure 1 for explanation of headings.

had left (at least one member with its head up) ($F = 6.6$, $N = 8$, $P = 0.05$) (Figure 4).

Growth

We found a significant degree of variation in measurements of weight, skull and tarsus when testing between all groups in an analysis of variance (ANOVA) model: significant at $P < 0.05$ or less for asymptote (A), growth constant (K) and growth inflection (I) for tarsus, for A and I for weight, and for A and K for skull (Table 2, Appendix 1). ANOVA revealed that the variance was produced from the STFR and PR goslings, which were lighter and smaller than the others; all measurements were similar for LTFR and NPR goslings.

Comparisons between STFR and PR goslings revealed significant degrees of variance for weight ($P < 0.05$ or less for A, K and I), skull ($P < 0.05$ or less for A and K), and tarsus ($P < 0.05$ or less for K and I), PR goslings being smaller. Generally, males were significantly heavier and larger than females in all groups (Table 1, Appendix 1).

Why were STFR and PR goslings lighter and smaller than the others? Several possibilities exist. These goslings were hatched predominantly from eggs from second clutches (8 of 9 in STFR and 3 of 10 in PR), which hatched up to 30 days later in the season. These groups were reared in smaller groups where the sex ratio was even; the sex ratio in the STFR and PR groups was 4 : 5 (males : females) and 5 : 5 respectively, whereas it was skewed towards males in the LTFR and NPR groups (10 : 2 and 9 : 2 respectively).

In order to exclude some of these confounding features, in the following year we reared six additional goslings with their parents (two families with three

Table 2. The mean values for asymptote (A), growth rate constant (K), and age in days at inflection (I) by rearing group. Also shown are the mean body measurements for the 1991 PR goslings (see text).

	Weight	(SD)	Skull	(SD)	Tarsus	(SD)
Asymptote (A)						
LTFR	2,275.8	(138.4)	96.9	(1.99)	86.1	(3.04)
NPR	2,216.2	(149.5)	95.7	(2.55)	86.3	(2.99)
STFR	2,086.0	(135.1)	94.1	(2.64)	83.2	(3.28)
PR	1,830.1	(140.9)	92.2	(2.49)	81.3	(3.39)
PR 1991	2,300.0	(101.0)	93.8	(2.18)	83.2	(2.34)
Growth constant (K)						
LTFR	0.091	(0.009)	0.052	(0.002)	0.091	(0.008)
NPR	0.087	(0.009)	0.053	(0.003)	0.092	(0.008)
STFR	0.101	(0.006)	0.054	(0.002)	0.092	(0.005)
PR	0.087	(0.016)	0.048	(0.004)	0.076	(0.006)
Inflection of growth (days) (I)						
LTFR	30.7	(1.61)	5.3	(1.16)	7.6	(0.97)
NPR	30.4	(1.79)	4.9	(0.65)	7.9	(0.57)
STFR	29.1	(1.30)	5.1	(0.81)	7.0	(0.74)
PR	32.6	(3.41)	5.2	(1.18)	8.6	(1.19)

For key to abbreviations see note to Table 1.

LTFR (N = 12, mean final age = 134.3, range 127–141), NPR (N = 11, mean final age = 135.4, range 130–141), STFR (N = 9, mean final age = 136.9, range 133–139), PR (N = 10, mean final age = 137.7, range 128–158), PR 1991 (N = 3, mean age = 80.3, range 80–81).

goslings each) in the same pens and provided them with ad lib food. Three of these were from second clutches. The sex ratio was 4 : 2. The parent body sizes were similar so genetic inheritance was ruled out.

Figure 5 illustrates that the 1991 PR goslings in an ad lib food situation were heavier and larger than 1990 PR goslings in a free-range situation (ANOVA, $P = 0.0001$ for weight, skull, and tarsus, $N = 57$, $df = 1$). There was a significant interaction effect across age and group for gosling weight, therefore one-way analyses were carried out for each age group. These were significant for all but the last age group (Appendix 2). The weights for the 1991 PR goslings were greater than those for LTFR, NPR, STFR and PR goslings.

This means that goslings reared in small groups that have equal sex ratio, which are from second clutches in the later part of the season, can become as heavy as those reared under the opposing situations. Therefore, the amount of food and size of rearing area may have influenced body size development. The fact that STFR goslings were also smaller in size in spite of having ad lib food available could also mean that goslings reared in smaller groups do not grow as large. This could arise if feeding trays were monopolized by the dominant siblings.

Discussion and management implications

We have discovered some significant links between rearing experience and subsequent behaviour traits of Nene goslings. Parent-reared birds are dominant

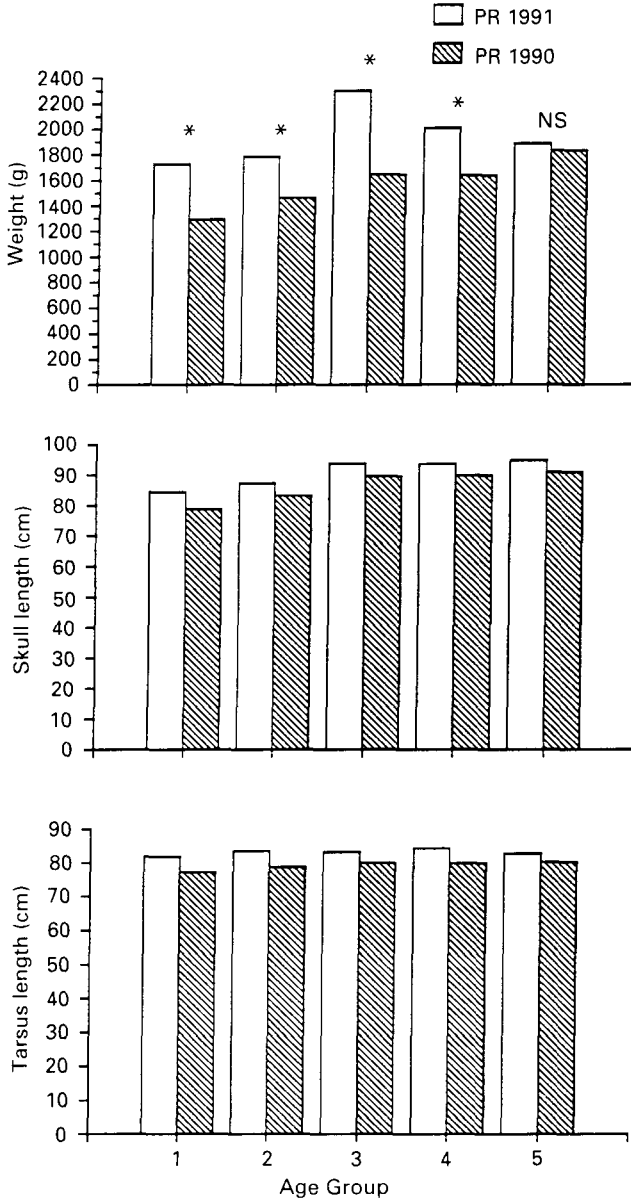


Figure 5. The mean weight, skull size, and tarsus length of PR birds in an ad lib food vs. free-range situation. * $P=0.0001$.

over goslings raised without parents or goslings raised in sight of adults. Parent-reared goslings associate with adult flock members sooner, and display higher degrees of vigilance for longer periods than other goslings. Parent-reared goslings avoid rather than approach predators, in this case a dog. Rearing regime (with or without parents or foster parents) does not appear to effect growth rates. We suggest, therefore, that goslings that are reared with parents will be better able to cope when released in the wild.

This suggestion is founded on the adaptive significance of the behaviour traits that we measured: social encounter skills, flock integration and vigilance. Social skills are perhaps most useful when geese compete for food (Teunissen *et al.* 1985, Black and Owen 1989b), mates and nesting territories (Collias and Jahn 1959, Owen and Wells 1979). Mixing well with flock members can have implications on detecting and avoiding predators and finding food (Pulliam and Caraco 1984, Black 1988). Being vigilant for predators can increase survivability (Kenward 1978) and can allow pair-bond partners adequate time to feed (Lamprecht 1989). Vigilance is a significant part of parental investment (Lazarus and Inglis 1978, Black and Owen 1989a). In another monogamous species, the Grey Partridge *Perdix perdix*, females preferentially choose the most vigilant male to mate with (Dahlgren 1990).

In order to survive and reproduce in Hawaii, young Nene released from captivity will have to find food, avoid predation and compete and mix with other Nene. The ability to join adult Nene in the wild may be beneficial in learning where to find food and when foods become available (e.g. berry emergence, etc.), although avoiding predators is perhaps the most prudent skill for a gosling to be equipped with prior to release. The vast majority of mortalities and nest failures are thought to be predator-related, compounded by small body reserves (Banko 1988). The fact that all gosling types, except the PR goslings, were decoyed by the dog, offers some explanation why Nene are susceptible to predation in the wild. Another example occurred in 1987 when a wild fox *Vulpes vulpes* got through the perimeter fence at Slimbridge. It took a disproportionate number of Nene over other waterfowl, because they gathered together and apparently approached the fox. These Nene were reared without parents.

A parallel study on Grey Partridges also quantifies the link between parent-rearing and adaptive behaviours. Dowell (1988, 1989) showed that parent-reared chicks, as opposed to chicken-reared or sibling-reared chicks, showed significantly longer bouts of vigilance. The partridges learned the anti-predator responses of their parent or foster-chicken parents, the latter being inappropriate responses. In addition, parent-reared partridges chose roost-sites most similar to those of wild partridges.

In an avicultural sense, parent-rearing is not the most practical method. This is mainly due to competition for spaces in breeding facilities and because fewer goslings are produced with the method. In addition, the anticipated practice at the Hawaiian breeding centre of hatching eggs sent from support breeding centres (like the Wildfowl and Wetlands Trust) will mean that the "foster" parent option should continue to be improved on.

It is unclear from our results which "foster" parent regime is best or whether rearing in view of adult pairs improves the goslings' adaptive behaviours above the level achieved by goslings reared without parents (see Table 3). STFR goslings ranked second in dominance and flock integration while LTFR goslings ranked last. Perhaps the STFR goslings ranked better because they were reared in small groups of three or four goslings as opposed to the larger groups as found in LTFR and NPR groups. It is possible that they performed better in aggressive interactions with flock members because their dominance rank order was well established among their siblings. Based on three studies on the development of social ranks in geese, it takes longer for the order to become

Table 3. The order in which goslings reared under different regimes rank in adaptive behaviours

Dominance	Flock integration	Vigilance	
		Proportion	Duration
PR	PR	PR	PR
STFR	STFR	LTFR	NPR
LTFR/NPR	NPR/LTFR	NPR	LTFR
		STFR	STFR

settled in larger groups (Radesater 1974, Stahlberg 1974, Black and Owen 1987). Perhaps STFR goslings integrated sooner with adults after release because they travelled in the small groups that they were raised in, whereas LTFR and NPR goslings travelled in the larger groups that they were raised in. STFR goslings ranked last in being vigilant after experiencing a predator and LTFR goslings behaved similarly to NPR goslings (see Table 3).

Our experimental design should be improved on so that the confounding feature of group size can be assessed. For example, the optimal group size may prove to be one that is small enough to enable quick integration with adult Nene and still large enough for the group to detect and avoid predators appropriately. In the mean time, we would encourage aviculturists to offer as much "foster" adult experience to naive goslings as possible. Increasing exposure to adults beyond the 15th day (e.g. the current Olinda regime) will strengthen the possibility of goslings learning appropriate behaviours (e.g. LTFR goslings are more vigilant than STFR goslings). If an amenable pair or group of adults can be housed together with a group of goslings perhaps the learning experience can be enhanced.

Another prudent line of investigation on Nene prior to release is in "creative training", i.e. introducing birds to "wild-like" experiences. The most successful reintroduction programmes are those that involve some sort of training programme, hacking, foster-rearing, etc. (Temple 1978, Cade 1986). Ellis *et al.* (1978) found that training and fostering increased the survival rate of Masked Bobwhite *Colinus virginianus ridgwayi* chicks released from captivity. Further studies are needed into the learning and imprinting on captive diets. There is some indication from Sandhill Cranes *Grus canadensis pulla* that captive diets influence food choice after release (Zwank *et al.* 1988).

It is clear from our results on body measurements that birds reared with ad lib food will obtain larger body sizes. In wild goose flocks, final body size is also related to food quality or abundance (Cooch *et al.* 1989, Larsson and Forlund 1991). Producing large-bodied Nene, however, may not necessarily be prudent, as smaller geese may be selected for in some years and situations (see review in Cooch *et al.* in press). In our study, the parent-reared goslings which grew in the free-range situation apparently obtained less food since they shared the space with many other geese (Nene and other species). It would perhaps be prudent for aviculturists to ensure that some competition for food be encouraged while ensuring that appropriate amounts are obtained for adequate growth rates.

Reintroduction and restocking programmes are often our last tool to be used to save critically endangered birds (Black 1991). Reintroductions that have failed

have frequently involved releases of inexperienced captive-bred birds (Fyfe 1978, Witteman and Pimm 1991). Reintroduction is an expensive and labour-intensive procedure (Cade 1986, Kleiman 1989). It is vital that resources are capitalized on by only releasing birds which will be able to cope with conditions in the wild.

Acknowledgements

We are extremely grateful to Andrew Coughlan for his invaluable assistance with biometrics and rearing goslings. We also thank Mario Bertuca, Derek Callaghan, Duane Green, Helen Gummer, Emma Linton, Clive Peters, Thomas Waite, and especially Steve Ridgill, Mike Bell and Nigel Jarrett for their practical assistance. Comments from Paul C. Banko, Fern Duvall and Myrfyn Owen significantly improved the manuscript.

Appendix 1. Analysis of variance table of probabilities for rearing effects on growth weights of rearing regimes. A = the asymptotic size, K = the growth rate constant, and I = the age in days at inflection.

	df	P			Group
		A	K	I	
Weight					
Sex	1	0.039*	0.394	0.299	LTFR/NPR
Group	1	0.147	0.986	0.456	
Sex	1	0.086	0.868	0.924	STFR/PR
Group	1	0.001*	0.041*	0.014*	
Sex	1	0.007*	0.502	0.589	All
Group	3	0.000*	0.070	0.011*	
Skull					
Sex	1	0.000*	0.009*	0.090	LTFR/NPR
Group	1	0.054	0.991	0.839	
Sex	1	0.000*	0.400	0.024*	STFR/PR
Group	1	0.008*	0.001*	0.957	
Sex	1	0.000*	0.014*	0.005*	All
Group	3	0.000*	0.000*	0.791	
Tarsus					
Sex	1	0.002*	0.542	0.002*	LTFR/NPR
Group	1	0.689	0.840*	0.047*	
Sex	1	0.017*	0.934	0.027	STFR/PR
Group	1	0.114	0.000*	0.002*	
Sex	1	0.000*	0.629	0.000*	All
Group	3	0.034*	0.000*	0.000*	

* $P < 0.05$.

Appendix 2. One-way analysis of variance on the effect of group (ad lib food vs. free-range) on the weight of PR goslings by age group (df = 1)

	F-ratio	P	N
Age Group = 1	23.168	0.001	11
Age Group = 2	5.555	0.040	12
Age Group = 3	36.471	0.001	9
Age Group = 4	14.028	0.003	14
Age Group = 5	0.489	0.502	11

Free-range group: Age Group = 1 (mean age = 43.8, range 42–44); Age Group = 2 (mean age = 50.8, range 49–51); Age Group = 3 (mean age = 79, no range); Age Group = 4 (mean age = 85.8, range 84–86); Age Group = 5 (mean age = 121.6, range 121–126).

Ad lib food group: Age Group = 1 (mean age = 42, no range); Age Group = 2 (mean age = 49, no range); Age Group = 3 (mean age = 80.3, range 80–81); Age Group = 4 (mean age = 86.2, range 85–88); Age Group = 5 (mean age = 123.3, range 123–124).

References

- Baldwin, P. H. (1945) The Hawaiian Goose, its distribution and reduction in numbers. *Condor* 47: 27–37.
- Banko, P. C. (1988) Breeding biology and conservation of the Nene, Hawaiian goose (*Nesochen sandvicensis*). Ph.D. diss., University of Washington, Seattle.
- Banko, W. E. and Elder, W. H. (1989) Population histories: species accounts, subgrassland birds: Hawaiian Goose, Nene. University of Hawaii and Manoa. Unpublished.
- Beck, B. B., Castro, I., Kleiman, D. G., Dietz, J. M., and Rettberg-Beck, B. (1988) Preparing captive-born primates for reintroduction. *Internatn. J. Primatol.* 8: 426.
- Berger, A. J. (1978) Reintroduction of Hawaiian geese. Pp. 339–344 in S. A. Temple, ed. *Endangered birds: management techniques for preserving threatened species*. Madison: University of Wisconsin Press, and London: Croom Helm.
- Black, J. M. (1988) Preflight signalling in swans: a mechanism for group cohesion and flock formation. *Ethology* 79: 143–157.
- Black, J. M. (1990) The Nene recovery initiative. The Wildfowl and Wetlands Trust and the Hawaiian Department of Forestry and Wildlife, unpublished.
- Black, J. M. (1991) Reintroduction and restocking: guidelines for bird recovery programmes. *Bird Conserv. Internatn.* 1: 329–334.
- Black, J. M. and Barrow, J. H., Jr. (1985) Visual signalling in Canada geese for the coordination of family units. *Wildfowl* 36: 35–41.
- Black, J. M. and Owen, M. (1984) Importance of family unit to Barnacle Goose *Branta leucopsis* offspring – a progress report. *Nor. Polarinst. Skr.* 181: 79–85.
- Black, J. M. and Owen, M. (1987) Determinants of social rank in goose flocks: acquisition of social rank in young geese. *Behaviour* 102: 129–146.
- Black, J. M. and Owen, M. (1989a) Parent–offspring relationships in wintering barnacle geese. *Anim. Behav.* 37: 187–198.
- Black, J. M. and Owen, M. (1989b) Agonistic behaviour in barnacle goose flocks: assessment, investment and reproductive success. *Anim. Behav.* 37: 199–209.
- Black, J. M., Duvall, F., Hoshide, H., Mederios, J., Natividad Hodges, C., Santos, N. and Telfer, T. (1991) The current status of the Hawaiian Goose *Branta sandvicensis* and its recovery programme. *Wildfowl* 42: 149–154.
- Boag, P. T. (1987) Effects of nestling diet on growth and adult size of Zebra Finches (*Poephila guttata*). *Auk* 104: 155–166.
- Cade, T. J. (1986) Reintroduction as a method of conservation. *Raptor Res. Rep.* 5: 72–84.

- Collias, N. E. and Jahn, L. R. (1959) Social behavior and breeding success in Canada geese *Branta canadensis* confined under semi-natural conditions. *Auk* 76: 478–509.
- Cooch, E. G., Lank, D. B., Rockwell, R. F. and Cooke, F. (1989) Long-term decline in fecundity in a Snow Goose population: evidence for density-dependence? *J. Anim. Ecol.* 58: 711–726.
- Cooch, E. G., Lank, D. B., Dzubin, A., Rockwell, R. F. and Cooke, F. (in press) Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. *Ecology*.
- Dahlgren, J. (1990) Females choose vigilant males: an experiment with the monogamous grey partridge, *Perdix perdix*. *Anim. Behav.* 39: 646–651.
- Devick, W. S. (1981a) Status of the Nene population of the Island of Hawaii between 1975 and 1980. Unpublished report to DOFAW-DLNR, Hawaii.
- Devick, W. S. (1981b) Status of the Nene population on Maui between 1975 and 1980. Unpublished report to DOFAW-DLNR, Hawaii.
- Dowell, S. (1988) Some effects of the method of rearing on the behaviour and ecology of grey partridges. *The Game Conservancy 1987 Annual Review*: 125–132.
- Dowell, S. (1989) Rearing partridges that will avoid predation. *The Game Conservancy Review*: 98.
- Elder, W. H. and Woodside, D. H. (1958) Biology and management of the Hawaiian goose. *Trans. North Amer. Wildl. Conf.* 23: 198–215.
- Ellis, D. H., Dobrott, S. J. and Goodwin, J. G., Jr. (1978) Reintroduction techniques for masked bobwhites. Pp.345–354 in S. A. Temple, ed. *Endangered birds: management techniques for preserving threatened species*. Madison: University of Wisconsin Press, and London: Croom Helm.
- Fyfe, R. W. (1978) Reintroducing endangered birds to the wild: a review. Pp.323–329 in S. A. Temple, ed. *Endangered birds: management techniques for preserving threatened species*. Madison: University of Wisconsin Press, and London: Croom Helm.
- Gassmann-Duvall, R. (1987) An acute *Cyathostoma bronchialis* outbreak in the Hawaiian goose and other parasite findings. Pp.61–68 in *Proceedings of Conference of Avian Veterinarians and American Association of Zoo Veterinarians*. Oaha, Hawaii.
- Kear, J. and Berger, A. J. (1980) *The Hawaiian goose: an experiment in conservation*. Vermillion, S.D.: Buteo Books.
- Kenward, R. (1978) Hawks and doves: attack success and selection in goshawk flights at wood pigeons. *J. Anim. Ecol.* 47: 449–460.
- Kleiman, D. (1989) Reintroduction of captive mammals for conservation: guidelines for reintroducing species into the wild. *BioScience* 39: 152–161.
- Lamprecht, J. (1989) Mate guarding in geese: awaiting female receptivity, protection of paternity or support of female feeding? Pp.48–66 in A. E. Rasa, C. Vogel and E. Voland, eds. *The sociobiology of sexual and reproductive strategies*. London: Chapman and Hall.
- Larsson, K. and Forslund, P. (1991) Environmentally induced morphological variation in the barnacle goose, *Branta leucopsis*. *J. Evol. Biol.* 4: 619–636.
- Lazarus, J. and Inglis I. R. (1978) The breeding behaviour of the Pink-footed goose: parental care and vigilant behaviour during the fledgling period. *Behaviour* 65: 62–87.
- Madsen, J., Bregnballe, T. and Mehlum, F. (1989) Study of the breeding ecology and behavior of the Svalbard population of light-bellied brent goose (*Branta bernicla hrota*). *Polar Research* 7: 1–21.
- Martin, P. and Bateson, P. (1986) *Measuring behaviour: an introductory guide*. Cambridge: Cambridge University Press.
- Morin, M. and Walker, R. (1986) The Nene restoration plan. DLNR-Division of Forestry and Wildlife. Unpublished report.

- Owen, M. and Wells, R. (1979) Territorial behaviour in breeding geese – a reexamination of Ryder's hypothesis. *Wildfowl* 30: 20–26.
- Pulliam, H. R. and Caraco, T. (1984) Living in groups: is there an optimal group size? Pp.122–147 in J. R. Krebs and N. B. Davies, eds. *Behavioural ecology: an evolutionary approach*. Second edition. Oxford: Blackwell Scientific Publications.
- Radesater, T. (1974) Form and sequential associations between the triumph ceremony and other behaviour patterns in the Canada Goose *Branta canadensis* L. *Ornis Scand.* 5: 87–101.
- Ricklefs, R. E. (1984) Components of variance in measurements of nestling European starlings (*Sturnus vulgaris*) in southeastern Pennsylvania. *Auk* 101: 319–333.
- Ricklefs, R. E., Bruning, D. F. and Archibald, G. W. (1986) Growth rates of cranes reared in captivity. *Auk* 103: 125–134.
- Smith, J. D. (1952) The Hawaiian Goose (Nene) restoration program. *J. Wildl. Mgmt.* 16: 1–9.
- Stahlberg, B. M. (1974) The development of rank order and aggressiveness in a group of juvenile greylag geese. *Wildfowl* 25: 67–73.
- Stone, C. P., Walker, R. L., Scott, J. M. and Banko, P. C. (1983) Hawaiian goose research and management – where do we go from here? *'Elepaio* 44: 11–15.
- Temple, S. A. (1978) Reintroducing birds of prey to the wild. Pp.355–363 in S. A. Temple, ed. *Endangered birds: management techniques for preserving threatened species*. Madison: University of Wisconsin Press, and London: Croom Helm.
- Teunissen, W., Spaans, B. and Drent, R. (1985) Breeding success in brent in relation to individual feeding opportunities during spring in the Wadden Sea. *Ardea* 73: 109–119.
- Wittman, G. J. and Pimm, S. L. (1991) The risk of extinction: lessons to be learned from introduced species. Unpublished.
- Zwank, P. J., Geaghan, J. P. and Dewhurst, D. A. (1988) Foraging differences between native and released Mississippi sandhill cranes: implications for conservation. *Conserv. Biol.* 2: 387–390.

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