Constraints on productivity of wild Nene or Hawaiian Geese *Branta sandvicensis*

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I investigated constraints on the productivity of wild Nene on Hawaii and Maui during 1978-81. These populations were composed largely of captive-reared birds. Recruitment of young was low. Of 140 breeding attempts, 36% resulted in successful nests and 7% produced fledglings. Annual productivity was limited because: 1) relatively few available pairs attempted to breed (58% on Hawaii; 46% on Maui), 2) average rate of nest success was low (44%), and 3) gosling survival was low (<39%). Low incidence of nesting suggests that many females could not accumulate sufficient body reserves for egg-laying and incubation due to poor foraging conditions or poorly developed foraging skills. Nest failure was high due to predation on eggs and incubating females by the introduced mongoose. Gosling mortality was high because of poor foraging conditions near many nests, forcing broods to travel over rugged, volcanic terrain to distant rearing areas. In addition, some goslings were killed by predators. Nene populations would benefit most from improved foraging opportunities for adult females and goslings and from reduced predator populations.

Introduction

The Nene remains a species at risk, despite over 30 years of captive propagation and releases to the wild. Although the release of over 2100 captive-reared birds since 1960 prevented the Nene's imminent extinction, wild populations decline when releases are curtailed (Devick 1981a). There has long been a need for field studies of factors limiting productivity in wild populations, since much of what is known about the breeding biology of this tropical, oceanic goose has been derived from captive flocks in Hawaii and England (Kear & Berger 1980).

Some characteristics of wild Nene *Branta sandvicensis* breeding behaviour suggest that productivity potentially could be high. For example, wild Nene are reproductively viable for many years; fertile eggs are laid by females ranging from two to at least 14 years of age and eggs are fertilized by males ranging from two to at least 19 years of age. In addition, wild Nene breed during about half of the year, and they sometimes renest after the loss of the first clutch (Banko 1988).

However, other aspects of Nene breeding behaviour indicate low productivity. For example, clutches of wild Nene do not exceed six, and eggs are very large relative to body size (Banko 1988). In addition, recruitment of wild young into the population is low. To help understand this problem, I report here on trends in productivity of wild Nene, with emphasis on frequency of breeding attempts and success of nests and broods.

Methods

I studied Nene breeding ecology from 1978 to 1981 in and adjacent to Hawaii Volcanoes National Park (HAVO) on the Island of Hawaii and in Haleakala National Park (HALE) on the Island of Maui. On Hawaii, I worked on Mauna Loa volcano in the Keauhou Nene sanctuary and adjacent land in HAVO at 1700-2300 m elevation. I also worked on Kilauea volcano from near sea level to the summit at 1238 m. On Maui, I studied Nene primarily in the eastern half of Haleakala Crater at 1525-2260 m elevation. I also worked on the outer slopes of Haleakala volcano on the north and east rim at 2130-2550 m and in the vicinity of park headquarters at 2135 m elevation.

My study sites were situated on relatively young volcanic substrates. The vegetation was generally sparse, especially on Kilauea where acidic rainfall, produced from volcanic fume, inhibited plant growth over a large area known as Kau Desert. Nene also occupied pastures and a golf course that were adjacent to nesting areas on Hawaii. A small pasture was also present at Paliku in the eastern end of Haleakala Crater. Paliku pasture differed from the pastures on Hawaii by being more lush due to greater rainfall and less grazing pressure.

Approximately 65% of the Mauna Loa Nene population was captive-reared and banded with unique colour combinations or numerals, allowing me to monitor the breeding status of known individuals between years. I monitored the breeding status of unmarked Nene (wild-reared) either by noting the band combination of the mate, or when mates were also unmarked (e.g. approximately 14% of Mauna Loa pairs), by the area where pairs were breeding. I assumed that there was insignificant band loss during the study, that unbanded birds had the same mates each year, and that unbanded pairs occupied the same nesting areas each year. These assumptions were probably seldom violated, based on my observations of banded pairs. I excluded young birds (females <3 years, males <2 years) from analyses of breeding frequency in populations.

I searched for nests from November through April, but I observed females for evidence of breeding from October through June. I classified Nene as breeding if they were tending a nest or brood or if the female was gravid (had a greatly distended abdomen) or had an incubation patch. I examined females with 10-power binoculars from approximately 30 m to evaluate the amount of abdominal swelling and to look for an incubation patch. Females with greatly distended abdomens were about to lay eggs or were already laying. Females with an incubation patch (indicated by missing, uneven, or recently replaced feathers on the upper abdomen), had laid eggs and lined the nest with feathers. Incubation patches were no longer visible after May or June, when most females had moulted. To locate breeding pairs, I hiked through known or suspected nesting habitat looking for any Nene, but especially ganders that appeared to be guarding nests or broods. My trained Brittany spaniel helped me find birds and nests during 1979-81 on Hawaii and in 1981 on Maui. When I discovered nesting Nene, I removed the dog from the area to reduce disturbance to the geese. I then approached nests and suspected nest sites cautiously to avoid flushing the pair. The female and male flew from the nest site in only one instance, and they returned soon afterwards. All other females either walked a short distance away or remained on the eggs until I slowly reached my hand towards them and gently lifted them off the nest to inspect the eggs. I visited nests weekly to evaluate their status.

I considered nests to be wild if they were located outside breeding pens maintained for captive Nene. A successful nest was one in which at least one egg hatched. When several factors were involved, I classified nest failure on the basis of: 1) the most important factor to affect the clutch as a whole, or 2) the factor affecting the last fertile egg(s) in the clutch. Therefore, if a predator destroyed only part of a clutch and the female subsequently discounted incubation of the remaining eggs, I assigned the entire cause of nest failure to predation, because it contributed to or caused the desertion. Similarly, if a fertile egg failed to hatch because of embryo mortality, that factor took precedence over those resulting in earlier egg losses (e.g. egg breakage). A successful brood was one from which at least one gosling fledged.

I considered a nest to have been depredated if: 1) the female disappeared during incubation but her mate continued to associate with the nest for at least a day, 2) the female was dead and partly eaten, or 3) one or more eggs were broken (not cracked) or removed from the nest. Mongoose *Herpestes auropunctatus* predation was characterized by the style of egg breakage and frequent removal of eggs from the nest (Banko 1988).

Unless otherwise stated, I combined results from both islands and all years for analyses of breeding effort and nesting success to facilitate comparisons with other species. Statistical comparisons of breeding effort and nesting success between islands and years were not warranted because sampling effort was uneven, sample sizes were small, and samples were not independent between years. I included inactive nests in the analysis of nesting success because failure rates were similar for inactive and active nests.

Results

Breeding activity in the population

Some Nene did not breed because they did not have mates, but at least 80% of all wild birds were paired in most years on Hawaii and Maui (Table 1). Single birds were usually males. Unpaired birds of either sex sometimes formed trios by joining existing, or possibly incipient, pairs for at least one breeding season. In addition to two such wild trios, three unpaired, free-flying females nested with penned males that already had captive mates. Siblings twice formed pair bonds when other mates were probably not available. One sibling pair remained together for a season while the other remained together at least four years, but both produced broods.

The frequency of breeding (pair found with nest or brood, or female with incubation patch or greatly distended abdomen) seemed relatively low for individual pairs on Hawaii during the 2-year period 1978-79, when I was able to collect the most complete information for any population. Of 13 marked pairs (at least one sex banded; all banded birds ≥ 3 years old) observed in both years on Mauna Loa, six (46%) bred in both years, five (38%) nested in at least one year, and two (15%) failed to breed in at least one year. I could not determine the breeding status of 14 other marked pairs on Mauna Loa during the same 2-year period.

Annual breeding rates of wild pairs averaged 58% on Hawaii during 1978-81 (*n* = 15-47 pairs/year) and 46% on Maui during 1979-81 (*n* = 33-61 pairs/year) (Table 1). Annual breeding rates of populations were lower when unpaired birds were included in the analysis (range = 44-54% on Hawaii and 20-63% on Maui).

Table 1. Breeding activity among wild Nene on Hawaii and Maui. Breeding pairs were those with nests, broods, or females that had incubation patches or greatly distended abdomens; none nested in open-topped pens.

	Breeding season			
HAWAII	1978	1979	1980	1981
Individuals *n*	108	89	57	35
1) pairs *n*	47	39	22	15
% of individuals with mates	87	88	77	86
2) Pairs breeding *n*	24	24	13	9
% of pairs breeding	51	62	59	60
% of individuals breeding	44	54	46	51
MAUI		1979	1980	1981
Individuals *n*		80	155	99
1) Pairs *n*		33	61	41
% of individuals with mates		82	79	83
2) Pairs breeding *n*		8	23	31
% of pairs breeding		24	38	76
% of individuals breeding		20	30	63

Breeding success

Nest success (at least one egg hatched) and brood success (at least one gosling fledged) were low among wild Nene. Of 140 breeding attempts during 1978-81 on Hawaii and Maui, only 50 (36%) hatched one or more eggs and ten (7%) produced fledglings. Breeding attempts included 132 attempts by pairs and eight inactive nests not directly attributable to observed pairs (Table 2). Successful nests included 31 nests that I observed and 19 broods for which I did not know the nest location (undiscovered nests).

Of 70 wild nests that were observed (55 active, 15 inactive), 31 (44%) were successful (Table 3). There was no difference between islands in nest success rate. Egg predation by mongooses accounted for 24 (62%) of the 39 unsuccessful clutches.

Wild Nene tended to abandon their clutches when only partially destroyed by mongooses. Based on the size of toothmarks, I suspected mongooses of killing four incubating geese during 1978-81, and this represented 10% of 39 nest failures. A mongoose also probably killed a female during egg-laying.

In addition to predation, wild nests failed because of desertion, storms, egg breakage (apparently unrelated to predation), embryo mortality, accidental death of the female, and abnormally small eggs. One female died when she accidentally became mired in a pool of tar leaking from a barrel, thereby stranding her clutch.

Of 29 wild broods, ten (34%) produced at least one fledgling during 1978-81. The modal number of fledglings per brood was two and the maximum was three (n = 10 broods). Of 49 wild goslings (n = 29 broods), 19 (39%) survived to fledge during this 4-year period.

Causes of gosling mortality were difficult to document, but an intense mountain rainstorm, accompanied by high winds and low temperatures, apparently killed at least one gosling (A. Medeiros pers. comm.) and probably contributed to the disappearance of others. A brood drowned when they were unable to climb out of a livestock water trough (K. Belt pers. comm.). A hatchling with dry down died in the nest, perhaps accidentally smothered during brooding. Another hatchling was apparently killed and removed from the nest by a mongoose or other predator. A feral dog killed a gosling near its nest (G. Clarke pers. comm.). Predators were not always successful in taking young Nene, however, as a wild male was once observed chasing a mongoose away from his brood and mate (D. Peterson pers. comm.).

Of 14 wild goslings (n = 9 broods) that I weighed, low weight, weight loss, or a very slow growth rate was characteristic of all that died or disappeared (Banko 1988). Since these goslings appeared healthy otherwise and predation was not evident, inadequate nutrition was probably a primary or contributing factor. Another indication of the role of food quality and availability in gosling survival was the general association of successful wild broods with areas of pasture grass (Banko 1988). Families travelled to pastures or similar areas soon after hatching if grass was not abundant near the nest.

Discussion

Breeding activity in the population

Infrequent breeding attempts among pairs accounted in large part for the poor viability of Nene populations on Hawaii and Maui. Breeding was attempted by relatively few pairs during each year of my study and also during 1982, when only 11 (41%) of 27 wild pairs nested on Kilauea (Stone *et al.* 1983). However, annual estimates of breeding activity probably represent minima, because I could not regularly survey all potential nesting habitat or observe all pairs throughout each breeding season, especially on Maui. In addition, I found the nests or broods of only 31-78% of all females suspected of breeding in each year. On the other hand, I may have overestimated the number of breeding females by misinterpreting the appearance of some distended abdomens or, less likely, incubation patches. For example, some females with seemingly distended abdomens may not have been gravid. Of all breeding females in any given year, 13-46% were observed only with a distended abdomen (Table 2). In addition, 17-29% of all breeding females seemed to have an incubation patch, but I did not observe their nests or broods. Inactive (unattended) nests were another, although relatively small, potential source of imprecision in calculating breeding effort. I found seven unattended nests that probably were the efforts of females observed with a distended abdomen or incubation patch. However, I found eight other inactive nests whose owners were less evident. These nests may have belonged to females that I observed with a distended abdomen or incubation patch, or females that I did not suspect of breeding or never observed during the breeding season.

In contrast to annual breeding rates ranging from 20 to 63% of available pairs for Nene populations, MacInnes & Dunn (1988) reported much higher proportions (82-92%) of adult (≥ 3 years) Canada Geese *Branta canadensis* nesting each year (four populations studied, including small and large races). Prop *et al.* (1984) determined that even in poor years 74% of Barnacle Goose *Branta leucopsis* pairs laid eggs. Although

Table 2. Type of breeding activity associated with Nene pairs (nest or brood, distended abdomen, incubation patch, or inactive nest). Females with a distended abdomen were gravid and would soon lay or were already laying eggs. Females with incubation patches had completed laying eggs and may have been failed breeders.

	Breeding season			
HAWAII	1978	1979	1980	1981
Pairs breeding *n*	24	24	13	9
1) Pairs observed with nest/brood *n*	17	11	4	7
% of breeding pairs	71	46	31	78
2) Pairs not observed with nest/brood *n*	7	13	9	2
% of breeding pairs	29	54	69	22
a) Female gravid (distended abdomen) *n*	3	4	6	2
% of breeding pairs	12	17	46	22
b) Female with incubation patch *n*	4	7	0	0
% of breeding pairs	17	29	0	0
c) Female gravid but dead *n*	0	2	0	0
% of breeding pairs	0	8	0	0
d) Pairs linked to inactive nest *n*	0	0	3	0
% of breeding pairs	0	0	23	0
3) Inactive nest: pair not associated but nest potentially attributable to a pair in category 2 *n*	3	1	1	0
MAUI		1979	1980	1981
Pairs breeding *n*		8	23	31
1) Pairs observed with nest/brood *n*		4	13	22
% of breeding pairs		50	57	71
2) Pairs not observed with nest/brood *n*		4	10	9
% of breeding pairs		50	43	29
a) Female gravid (distended abdomen) *n*		0	5	0
% of breeding pairs		0	22	0
b) Female with incubation patch *n*		0	5	9
% of breeding pairs		0	22	29
c) Pairs linked to inactive nest *n*		4	0	0
% of breeding pairs		50	0	0
3) Inactive nest: pair not associated but nest potentially attributable to a pair in category 2 *n*		0	0	3

MacInnes *et al.* (1974) found that, like Nene, some older (≥ 4 years) Canada Geese never nested and others nested less than once per year during a 6-year period, the mean frequency of non-nesting was low (1 time/5.6-12.5 years) (MacInnes & Dunn 1988). Non-nesting rates for individual Nene were much higher (e.g. 15% of Mauna Loa pairs did not breed in at least one of two years).

Although methodological differences and sampling difficulties in Hawaii may have accounted for some of the disparity with Canada Goose studies, lower breeding activity in Nene populations was not attributable to the presence of large numbers of immature birds. More than half of the birds I studied were marked and were at least three to four years of age. Low annual recruitment of young into upland wild populations (Devick 1981a,b, Santos & Ueoka 1980, Ueoka 1978-88, Banko & Elder 1990, Hoshide *et al.* 1990, Black *et al.* 1991, this study) suggests that few unbanded Nene would have been less than three years old during the study.

I suspect that many Nene failed to nest primarily because females did not acquire sufficient body reserves for producing eggs. Other studies of geese have shown that body reserves affect breeding performance, including egg-laying and incubation ability (Aldrich & Raveling 1983, Prop *et al.* 1984, Hamann *et al.* 1986, Ebbinge 1989). Nene females that failed to lay eggs may not have fattened sufficiently due to poor quality or availability of foods, as suggested for Barnacle Geese (Prop *et al.* 1984). In addition, many captive-reared Nene may not have acquired adequate foraging skills prior to release.

Within a vestigial population on Mauna Loa, six (86%) of seven pairs of wild Nene nested during a single season (Elder & Woodside 1958). This small group of birds was composed only of wild-strain Nene; there were no captive-reared birds among them. This high nesting rate might only be an artifact of a limited sample size, or it might indicate superior habitat conditions existing at that time or superior foraging or social skills of wild-strain geese.

Smaller clutch size of wild Nene would also support the idea that light body reserves limited productivity (Hamann *et al.* 1986). In fact, I found that average clutch size of wild Nene was one less than for captives that had supplemental food (Banko 1988).

Some Nene, especially those reared in captivity and possibly having less developed social skills (Marshall & Black 1992), may not have bred because they could not find, attract, or maintain a suitable mate. The occurrence of sibling pair bonds and trios suggests that suitable mates are scarce in these small scattered populations.

Breeding success

Poor nesting success (44%) was another major constraint on wild populations during my study and more recently, when only 21% of 136 nesting attempts succeeded (Hoshide *et al.* 1990). In contrast, nesting success was higher in Canada Geese (mean = 70%; range = 21-89%; n = 11,865 nests) (Bellrose 1980). Predation by mongooses was the leading cause of nest failure in Nene (72%; n = 70 nests), and nest predation, especially by mammals, also was the leading factor in Canada Goose nest failure (48%; n = 2488 nests). Another indication of the mongoose's predatory capability was the removal of chicken eggs from 91% of the artificial nests (n = 328) that I placed in Nene breeding areas (Banko 1988). Nene eggs and incubating females were particularly vulnerable to mongooses due to low nest attentiveness. Nest attentiveness was low because female condition was poor during incubation and foraging conditions were poor near nests. Compared to captive Nene having access to supplemental food, wild females spent more time sleeping and feeding during incubation, and their mates were often inattentive or absent from nests (Banko 1988). Low nest attentiveness increased opportunities for mongooses to take eggs while nests were unattended or kill sleeping or unguarded females.

Table 3. Success rate of Nene nests (n = 70) and causes of failure on Hawaii and Maui during 1978-81.

	n	Percent
Successful nests	31	44
Unsuccessful nests	39	56
Predation on clutch	24	62
Predation on female	4	10
Other female mortality	1	3
Desertion	3	8
Storm	2	5
Egg breakage	2	5
Embryo mortality	2	5
Runt eggs	1	3

Little has been published concerning the survival rate and causes of mortality of young wild Nene in the years prior to captive rearing and release, but Munro (1944) was told that wild broods usually consisted of two goslings. Elder & Woodside (1958) found that two goslings per pair were fledged from six pairs in the uplands during one season. In that study, the only known case of mortality was a gosling that was probably killed by a mongoose. Even in recent years, broods of two are most common in the wild (Banko & Elder 1990, this study). Although I found inadequate nutrition to be the leading factor contributing to gosling mortality, Hoshide *et al.* (1990) determined that predation, especially by mongooses, was most important. Mongooses, feral house cats, and feral dogs have frequently been cited as predators of young (Kear & Berger 1980). The mortality rate of goslings reared in pens at HAVO and HALE, where predators were trapped and commercial ration was available, was 38% (n = 39) (Banko 1988). Although predators did not kill any pen goslings, inadequate nutrition probably was a factor, because many captive goslings lost weight or grew slowly prior to dying (Banko 1988).

My results and those of Banko & Elder (1990) and Hoshide *et al.* (1990) suggest that the survival rate of wild Nene goslings may be consistently the lowest of all geese. In contrast, wild Canada Geese fledge at a high rate, averaging 85% (n = 5959 successful nests, Bellrose 1980). In fact, the 39% survival rate of wild Nene goslings I observed probably represents a maximum value due to the greater likelihood of detecting fledglings rather than goslings that died before fledging. Active nests were most readily detectable for only about five weeks (laying and incubation periods), and young broods were mobile, secretive, and difficult to locate. However, I could distinguish young-of-the year for at least four months after the nesting season, because families often congregated at feeding areas, such as Ainahou (Hawaii) and Paliku (Maui) horse pastures. Gosling mortality was probably underestimated, therefore, because 18 of 19 fledglings were not seen prior to fledging (i.e. their nest was not found and they were not encountered as young goslings).

Management recommendations

Natural recruitment of young into wild Nene populations is so low that periodic releases of captive-reared birds will continue to be necessary to sustain populations in most areas, especially upland sites, for the near future. However, stocking wild populations should not be the primary management tool, since self-sustaining populations have yet to be established in the wild, despite the release of over 2100 captive-reared Nene by state and federal agencies since 1960. The results of my study indicate that improved foraging opportunities should increase the number of nesting attempts as well as the survival rate of broods, and more effective control of predators should improve success rates of nests and broods. Supporting this view is the rapid, natural growth of small, recently-established Nene flocks at lowland sites on Kauai and Hawaii (Keaau Ranch), where pasture grasses are abundant and predators are few (Black *et al.* 1991). Indeed, where foraging conditions are best and predators are maintained at reduced levels, Nene populations have fared best (Black *et al.* 1991). For example, despite the death of many Nene soon after their release in Haleakala Crater, Maui, the population has been relatively stable at over 100 individuals since 1977, when the last group of geese was released (Ueoka 1978-88, Banko & Elder 1990, Black *et al.* 1991). Wild young were recruited into the population at an average rate of 1.8 fledglings/year (range 0–8) during 1977-88 (Ueoka 1977-88, Banko & Elder 1990). The population has increased somewhat since 1980, largely because sprouting pasture grasses have been available continuously at Paliku and predator traplines have been maintained in recent years (Black *et al.* 1991, Natividad Hodges 1991). Research and management attention should be directed towards developing and implementing effective schemes for improving foraging opportunities and reducing predator populations throughout important portions of the Nene's range

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