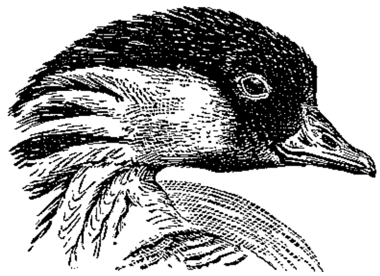
Foraging behaviour and energetics of the Hawaiian Goose *Branta sandvicensis*



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The Hawaiian Goose fed on 31 plant species; grasses predominated in most seasons, while berries were favoured during incubation. The relative amount of these foods in the diet varied between sexes, bird-class, area and date. Variation in breeding success within and between sub-populations was determined probably by local climate and subsequent plant phenology. We observed a seasonal decline in food quality and density, i.e. a decreasing protein content in grasses, a decline in density of grass seedheads and a decline in water content and density of berries. It is likely that this seasonal pattern restricts the period Hawaiian Geese have available for breeding, just as the spring flush of plant growth delimits the time for reproduction in arctic-breeding geese. At the Volcanoes study site, some of the breeding pairs supplemented their berry diet by flying to grassland some distance from the nest; at Haleakala, all incubating pairs used pastures. We argue that in order to save the goose, managers will have to employ a prolonged, intensive hands-on approach to management, by removing predators and creating and sustaining high-quality grassland habitats well into the future. Refuges should be located near to natural scrubland nesting habitat, as geese in these areas will continue to utilise the full range of foraging skills that characterise the species.

Keywords: Hawaiian Goose, Nene, Energetics, Foraging, Incubation, Diet

Without restocking the population of the Hawaiian Goose *Branta sandvicensis*, better known as the Nene, with captive-bred birds, numbers in the wild would rapidly decline (Black & Banko 1994). Low viability is caused by the combination of low productivity (Banko 1992) and low survival (Black *et al.* 1993). Poor availability of food is thought to be a major bottleneck in the birds' annual cycle (Baldwin 1947, Stone *et al.* 1983a, Banko 1992, Hoshide *et al.* 1990).

In 1990 a research programme was launched that aimed to understand the factors responsible for the poor performance of Nene in the wild (Black 1990, Black *et al.* 1991a). This paper focuses on the situation during the winter breeding season. We ask whether foraging conditions in the habitats that Nene use currently are sufficient for successful reproduction. We address the problem by quantifying the feeding performance of the geese in a stepwise process. First, by assessing how Nene spend the day we calculate the proportion of time needed for feeding and the effort that is used in foraging bouts. We assess whether certain foods are preferred or avoided by determining the Nene's diet and the distribution of food in the environment. By measuring the availability and rate of depletion of the food, we assess how many geese current habitats could support. Lastly, we calculate the nutritional value of the chosen diets in terms of daily energy intake, to detect at which stage the birds' energetics could inhibit successful reproduction.

We realize that our work is a small step towards understanding the ecology of the Nene and that much work is needed to solve all problems of its low productivity, but we think it is important at this stage to make our findings available for future research. Time is running out for the Nene (Black & Banko 1994).

For information on the current status of the 600 remaining geese and the conservation programme see Black *et al.* (1991a), Banko (1992), Black & Banko (1994), Black (in press). For background information on the Nene reintroduction programme, refer to Kear & Berger (1980).

Study areas and methods

The main data set was collected at Volcanoes National Park (**Figure 1**), 850-1220 m elevation, and the surrounding areas during

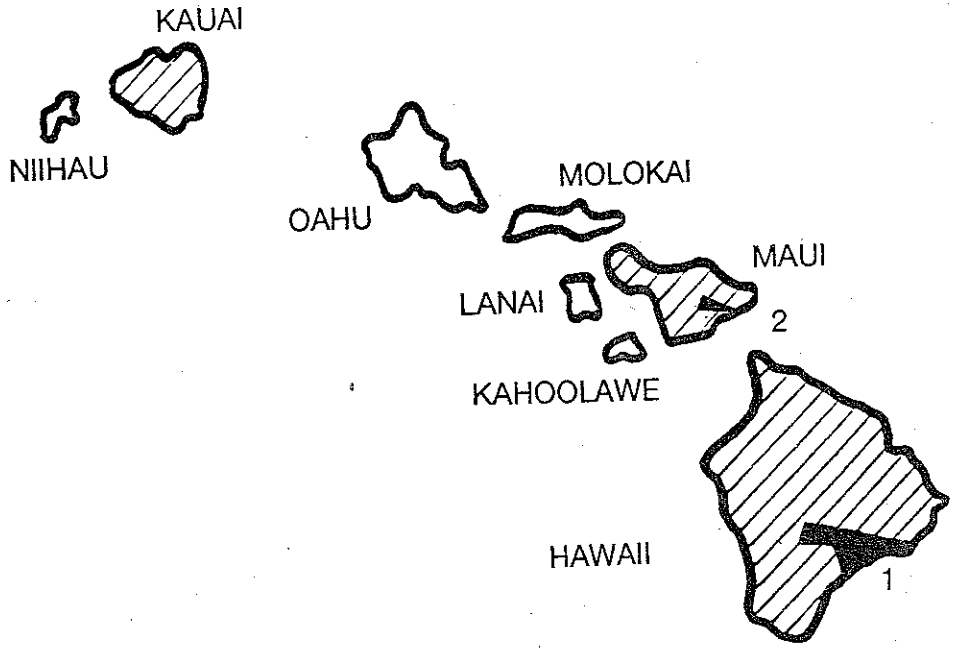


Figure 1. Map of the Hawaiian Island showing the main study sites; 1=Volcanoes National Park, 2=Haleakala National Park. Hatching indicates which islands are populated by Nene.

Table 1. Statistics of observed Nene pairs nesting at Volcanoes 1991- 92 and Haleakala 1992- 93.

Nest	Male	Age	Female	Age	Hatched	Fate of goslings
Volcanoes						
1 N Kau	674	4y9m	UNR		yes (2)	fledged
2&9 N Kau	*ZA		839	21y9m	no	abandoned
3 N Kau	705	2y	UNR		yes (3)	fledged
4 Crater	694	3y	+10/453	10y10m	no	failed
5 Crater	632	7y	648	6y	yes (3)	died
6 S Kau	*ZH	4y	*ZF	7y	-	-
7 S Kau	607	7y10m	704	2y	yes (2)	-
8 Crater	*YP	11m	651	6y	yes (1)	-
9 Crater	WR/RGY	3y10m	UNR	-	yes (2)	died
10 NE Kau	*ZU	-	*ZL	-	yes (1)	fledged
Haleakala						
1 Paliku	UNR	-	*CS	min 2y	yes (3)	
2 Paliku	UNR	-	UNR	-	yes (3)	1 predated
3 Paliku	*CP	4y	*FF	-	yes (1)	died
4 Paliku	*BS	min 12y	*BT	22y	-	-
5 Paliku	*CH	min 2y	UNR	-	yes (3)	2 died[a]
6&15 Paliku	*AD	-	*CY	min 2y	no	abandoned
7 Paliku	*BY	min 4y	?	-	no	abandoned
8 Paliku	*AP	min 2y	WY/WGB	14y10m	no	failed
9 Laulu	YR/-	15y	WR/B	14y9m	no	predated[b]
10 Oili puu	*AX	min 2y	*AC	min 2y	no	failed
11 Paliku	*AT	min 2y	*FA	-	yes (3)	all died
12 Puu Maile	UNR	-	UNR	-	-	-
13 Laulu	Red 3	min 3y6m	UNR	-	-	-
14 Laulu	UNR	-	UNR	-	yes (4)	1 died

[a] Third gosling removed to Olinda.
[b] Female and eggs were predated by mongoose.

the breeding season (November 1991 to January 1992). We concentrated on pre-breeders and non-breeders at Halfway House pasture and corral, Kapapala Ranch, Kipuka Nene Campground, and breeding geese nesting in the Kau Desert. Supplementary data were collected in upland areas (1500-2050 m elevation) at Kipuka Ainahou Sanctuary, Kahuku Ranch and Keauhou Sanctuary. As a reference to the performance of Nene at Volcanoes, additional data on time budgets and diet composition were collected at Haleakala National Park, Maui (**Figure 1**), during the

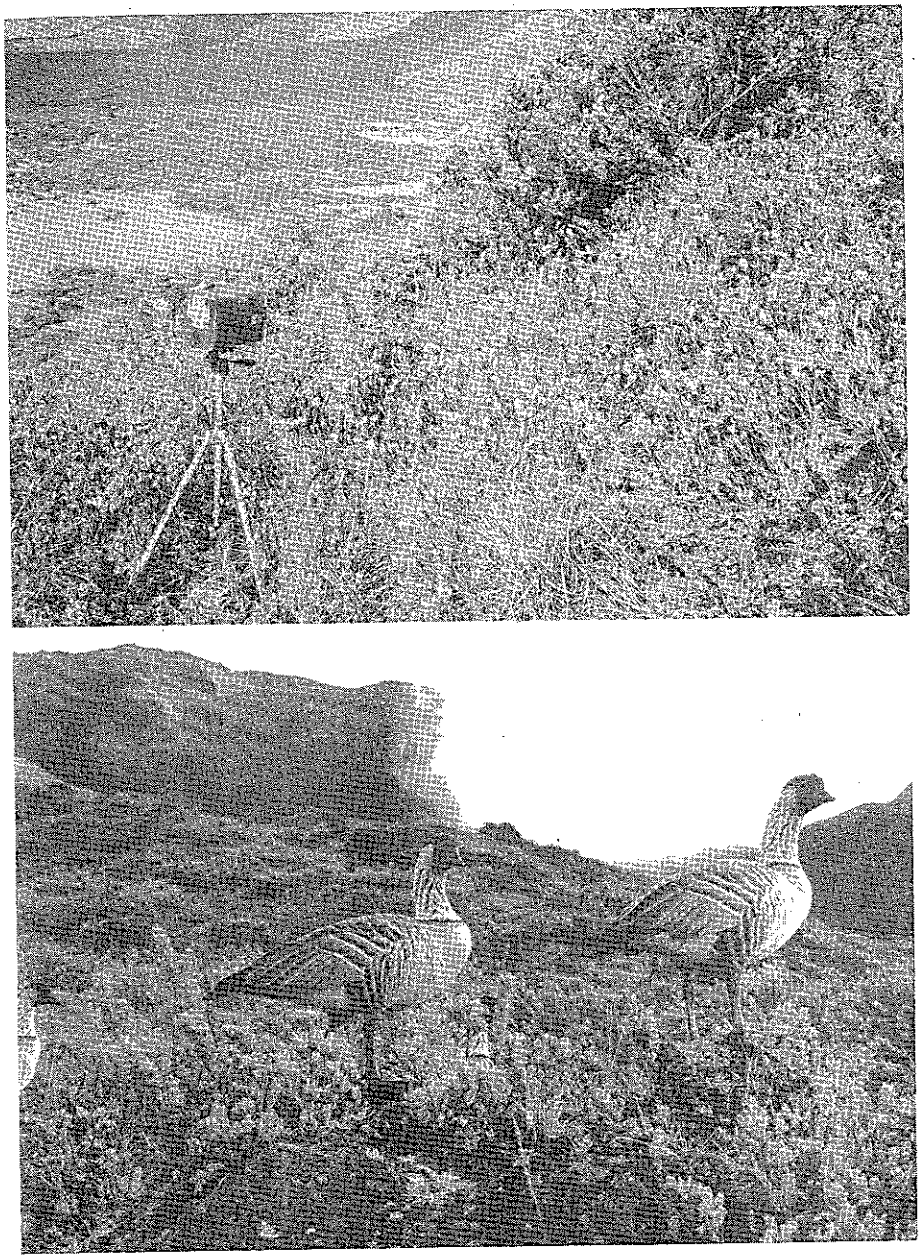


Figure 2A A super 8 camera pointing at a Nene nest under a large pukiawe bush *Styphelia tamaiameia* at Laie flats, one of the native grassland sites (mainly hairgrass *Deschampsia nubigena*) in Haleakala Crater, Maui. Figure 2B Un-banded Hawaiian Geese standing on lava rocks where ohelo seedlings *Vaccinium reticulatum* and pukiawe bushes were found. ***(Figure 2C follows on next page)***

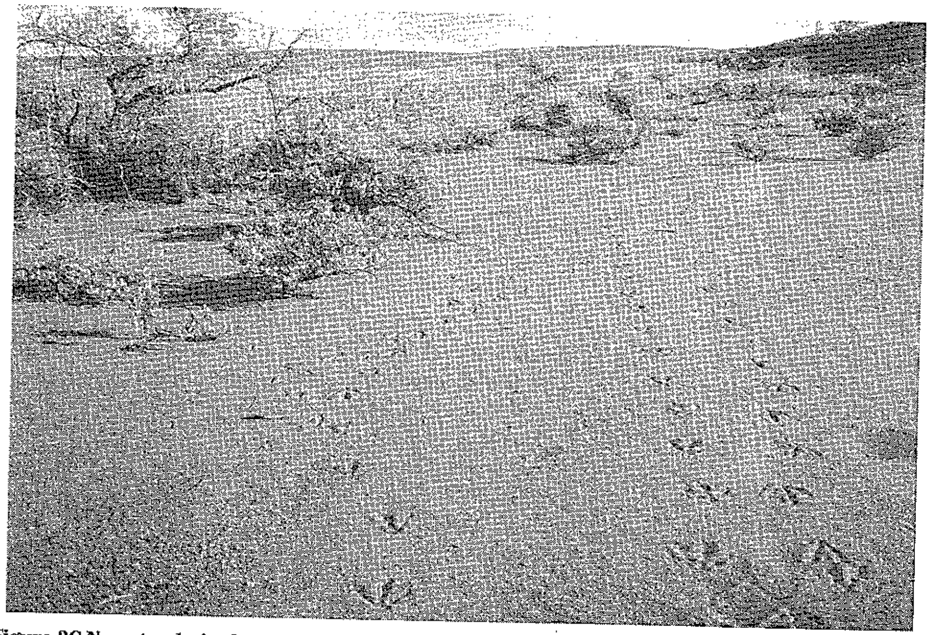


Figure 2C Nene tracks in the sand at Volcanoes National Park, Hawaii, leading from a nest site (nests 5 and 8) located in the scrubland, dominated by aalii bushes *Dodonaea sp.* and mollasses grass *Melinis minutiflora*.

breeding season (November 1992 to February 1993) and non-breeding season (July to September 1992). Study sites were (a) Paliku pasture (2000 m elevation), an area grazed by horses with a vegetation dominated by Yorkshire Fog *Holcus lanatus* and Kikuyu Grass *Pennisetum clandestinum*, and (b) Kuiki grassland, a smaller area vegetated by Yorkshire Fog and Hairgrass *Deschampsia nubigena*, located at 2500 m. The population sizes were about 135 at Volcanoes and 150 at Haleakala; there are about 600 Nene in the wild throughout the state (Black *et al.* 1991a, updated). We saw between two and 46 geese at any one time. For further details of these sites see (Banko & Manual 1982, Stone *et al.* 1983a & b, Hoshide *et al.* 1990, Banko & Elder 1990).

Most geese were marked individually with plastic rings (Darvic) readable from a distance. During the breeding seasons we monitored ten breeding pairs at Volcanoes and 14 at Haleakala (**Table 1**). The Nene in this sample bred between the ages of 11 months and 22 years (where ages are known). Thirteen of these pairs succeeded in hatching at least one gosling.

Activity patterns

During the breeding season, the activities of breeding birds were determined from 5 minute scans which were augmented by using either a super-8 camera or video, exposed at 1-1.5 minute intervals (**Figure 2**). The video was fitted with an infra-red device which enabled us to record activities of females at night as well. A total of six different pairs of nesting Nene at Volcanoes was observed. The following activities were included: on or off the nest (for females), feeding, vigilance (low and high level postures), loafing (sit and sleep), preening (including bathing) and social activities (triumph ceremony, aggression). The percentage of each activity was calculated for each sex. During recesses, females were followed continuously (see below). Some pairs flew to distant locations to feed. Because each pair used the same location throughout incubation, site choice was predictable, and a second observer waited for the birds at the distant site to follow them when they arrived. Flight times between the nest site and the distant foraging area were recorded. The observations of females allowed us to determine the number of incubation recesses per day and the total time spent off the nest. At the beginning of each recess, females produced one large dropping close to the nest. By collecting and counting these droppings on a daily basis, we had a second way of determining the number of recesses.

During the breeding and non-breeding season, the activities of non-breeders were determined from periodic scans, as above. At Haleakala, the behaviour of two discrete flocks was recorded. On five all-day sessions, the activity of each flock member was recorded every five minutes. Data from the same hour, over several days, were lumped. Records featuring birds of unknown sex were omitted.

A shorter study of a flock on Kauai (**Figure 1**), 0-50 m elevation, was made in August 1990. A flock of up to seven birds was monitored at 5-15 minute intervals throughout the daylight hours over two days. The sex of the Kauai birds was not known.

The Nene diet

Fragments in droppings were analyzed according to the procedure employed by Owen (1971), Owen & Kerbes (1971) and Owen (1975). All large berry seeds and grit particles were removed prior to microscopic investigation. Fifty fragments were identified in each sample using 100-400 magnification along several transects through each slide. Fragments were identified by comparison with photographs (x130 or x180 magnification) of nail-varnish impressions of the upper and lower epidermis of a range of plant species that were collected in Nene habitats. Direct comparison with dried plants samples was also useful.

For some analyses, fragments were assigned to broader plant categories (e.g. berry pulp, grass leaf, grass seed and herb). A mean per cent abundance was calculated for each species.

As the proportion of berry pulp in the droppings was correlated positively with the number of Pukiawe *Styphelia tameiameiae* seeds (R=0.313, *n*=204, *P*> 0.001), we assumed that berry pulp in the droppings was from Pukiawe.

Availability and production of important food plants

A quantitative assessment of vegetation around eight nest sites at Volcanoes National Park was made by counting the number of individuals of the main plant species in 5 x 100 m transects radiating out from each nest in four directions (N, E, S and W). The transects were subdivided into 5 x 5 m quadrates. At distances of 50-100 m from the nest, every other quadrat was omitted from the analysis. The four most numerous species: Pukiawe, Ohelo *Vaccinium reticulatum*, Aalii *Dodonaea viscosa* and Ohia lehua *Metrosideros sp* were split into the categories of small, medium and large. An index of bush density was calculated by multiplying the number of bushes of different size-classes, in each quadrat, by the following factors: large x 3, medium x 2 and small x 1. For each quadrat the percentage vegetation cover was estimated visually together with the percentage cover of sand, and bare rock/lava.

Measurements on blades of Beardgrass *Schizachyrium condensatum* were made by marking 16 individual shoots with small tapes or plastic rings, and recording, at intervals of 6-8 days, the length of all green leaves on the shoot. The sum of all green leaves per shoot, on a given date, was taken as a measure of availability. The growth rate was estimated by the length increment of the youngest two leaves between two successive measurements. Similar measurements were made on Kikuyu Grass shoots at Kapapala Pasture and Kipuka Nene Campground.

To determine the production of grass seedheads, ten plots (100 x 40 cm) were sampled on three occasions in December and January (Halfway House pasture). All seedheads (Rattail Grass *Sporobolus africanus*, Dallis Grass *Paspalum dilatatum*, Narrow-leaved Carpet Grass *Axonopus fissifolius* etc.) were marked, allowing recognition of newly produced ones. Using a dissecting microscope, numbers of seeds were counted per seedhead. The density of grass plants and seedheads was also recorded within 20x20 cm plots. The plots were located in cattle pastures (Kapapala Ranch) in a) slight depressions, b) gently sloping areas and c) steep slopes. A rough assessment of the 'lie of the land' indicated 20% depressions, 60% gently sloping and 20% steep. Nene used all three areas.

To determine the availability of berries over time, bushes of Pukiawe and Ohelo were marked individually in study areas at a cinder field (Keanakakoi Crater, Crater Rim Road) and in the Kau Desert (13 and 60 Pukiawe and ten and ten Ohelo bushes, respectively).

To determine the length of successive phenological stages of fruits on bushes, twigs with a cluster of flowers and/or berries were marked (35 ohelo twigs and 30 pukiawe twigs at the cinder field, and 44 pukiawe twigs in the Kau Desert). At intervals of five to eight days the number of items for each of the phenological stages was recorded. The stages distinguished were flower, unripe berry (green in Pukiawe, red in Ohelo), ripe berry and aged berry (brownish and starting to dry out). From successive records of all items on the same twigs, development could be reconstructed. The period of study was too short to determine directly (from individual items) the length of each phenological phase. Instead, the duration (D) for each phase (P) was calculated as $D_P = I*(1/(1-F_P))$, where I=interval in days between measurements, F_P =fraction of items staying in phase P over the interval. For an accurate estimate, the fraction F_P should be close to 0.5. Thus, for Pukiawe a comparison could only be made between the first and the last date of sampling. Ohelo had a more rapid development of berries and, for this species, calculations could be performed for two separate periods.

To measure growth rate of berries of Pukiawe, 61 berries on 19 different bushes were marked. Small plastic tapes with an identification number were placed around the twigs just below the berries. Each berry that was measured was marked with a small dot of Indian ink. At intervals of 6-8 days the diameter (width) of the berries was measured, and the colour noted.

The production (PR) of berries was calculated as PR=M+G, where M=mortality rate, estimated as the inverse of the duration of berries in the ripe phase (see above). G=growth rate, estimated from the availability plots (see above).

Availability of potential nest sites

Availability of potential nest sites was estimated in two areas in the Kau Desert (12 and 24 km^2), known to be core nesting areas for Nene. The identification of potential sites was based on the characteristics of a nest site as defined above, using the following criteria: 1) clusters of large shrubs or trees, and 2) open foraging areas near the nest (radius at least 100 m) with scattered berry shrubs (Pukiawe or Ohelo), intermingled with sandy areas with grasses or herbs (see below). In order to scan the large areas, aerial photographs were used for a first inventory. The pictures (approximate scale 1:25000) were studied by means of a stereoscope, which allowed detection of the larger bushes (more than about 1.5 m), that are important for providing cover. The smaller Pukiawe and Ohelo bushes could not be distinguished. Instead, to locate potential nest sites on the photographs, we relaxed the second criterion, looking for only the presence of sandy patches, which were easily visible on the photographs.

Food quality

To assess relative qualities of foods in different areas, we collected the parts of the plants that the Nene were eating. Samples were sorted, removing dead material, and dried at 50°C. Samples were analyzed for ash, fat, acid detergent fibre (ADF), neutral detergent fibre (NDF) and Nitrogen (using the Kjeldahl method, N x 6.25=crude protein). All berry types were analyzed for total sugars. Percentage water content was derived from wet and dry weights. Per cent carbohydrate was calculated by subtracting values for moisture, protein, NDF, fat and ash from 100. Where appropriate, dry weights were converted to ash-free dry weights. Digestibility of different food types was determined using ADF as a natural marker (Prop & Vulink 1992), using dropping samples which were composed largely of the remains of only one food species.

Foraging behaviour and food depletion

We placed hides close to nests or at vantage points overlooking areas that were frequently visited (e.g. Devastation Trail), in order to keep disturbance to a minimum. During incubation recesses, the geese were followed and observed at a distance through a telescope. Commentaries of the birds' behaviour were recorded on a cassette recorder. All changes in activities were noted: grazing, standing alert, walking, preening, or out of view. All pecks were recorded, where possible, with information on the type of food eaten and the level of the head during the peck. Levels distinguished were relative to the body of the goose: 1=up to the knee, 2=up to the breast, 3=up to head level, body not stretched, 4=bove the head, body stretched (vertical). The amount of time birds spent at each

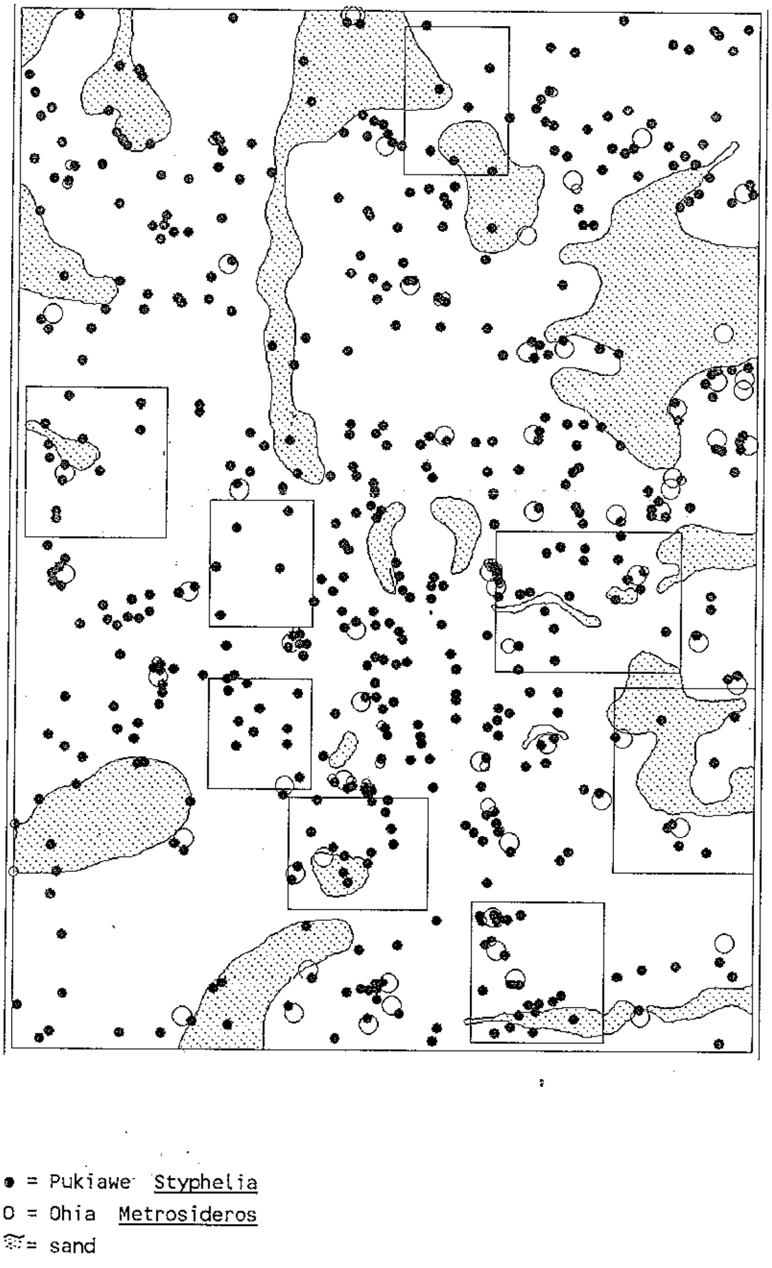


Figure 3. Distribution of Pukiawe bushes and Ohia lehua trees at Nene nest #3 in the Kau Desert (location of nest at bottom left corner of plot, the dimensions are 50×70 m). Squares indicate sampling plots for Pukiawe bushes.

berry bush was recorded. Every other step was noted. Step length was estimated by measuring the distance between footprints in the sand (**Figure 2c**).

To relate feeding behaviour to food availability, 12 plots with an average size of 10x10 m were selected close to one of the nests studied (**Figure 3**). The Pukiawe bushes within the plots were marked with a stick with an identification number readable from the observation position. The size of the bushes was measured (see above) and, on goose observation days, the number of ripe berries on each of the bushes was counted. To relate peck rates to berry densities, the average density during a visit was calculated.

Individual grass plants were marked with small plastic rings and measured at weekly intervals throughout the study periods. Between 10 and 30 branches of Ohelo and Pukiawe bushes were marked individually and the number of young, ripe and old berries were counted at weekly intervals.

To assess the grazing pressure on Pukiawe berries, the number of ripe berries per bush was recorded along transects from nest 3. Sampling stations were at a distance of 20 to 250 m from the nest. At each site, a minimum of ten Pukiawe bushes were measured. The width (W) and height (H) of these bushes were also measured. To test which combination of W and H described the size of a bush best, similar measurements were collected at sites which had not been visited by geese (far from known nests and/or where there were no droppings or footprints of geese). The measure for bush size was such that (1) the relationship between the number of berries and size of a bush was linear, and (2) the slope of the relationship between density of the berries (i.e. number of berries divided by the size) and size of the bush was zero. Several measures for size were tested (WxH, W^{2}xH, WxH^2, (WxH)^x, W+H, ≠WxH, Wx≠H). The measure, (WxH)$^{0.75}$, satisfied both criteria best.

Food intake and energetics

The intake rate (IR g min^{-1}) was calculated following Prop & Deerenberg (1991):

IR= PF x LT x NL x W, where

PF=peck frequency, estimated by recording the time needed for 50 pecks for geese feeding in the immediate vicinity of the study plots; times were converted into pecks.min^{-1}.

LT=average leaf size taken, mm (derived from marked shoots, see above).

NL=number of leaves taken per peck, derived from close inspection of the sward to distinguish separate bites.

W=weight of individual leaves.

For the larger items, such as mature grasses with seedheads, on which several peck-movements were taken, we determined the number of pecks per item. Leaves, seedheads and berries were compared before and after grazing by Nene. Similar-sized 'bites' were also removed by hand. To determine the size of leaves that were removed, we lined up and matched the top of a grazed leaf on an ungrazed leaf of similar size and width; a method that proved quite accurate, r^2=0.88, *n*=31). Berries and seedheads were collected from all study areas. Samples were dried overnight at 90°C and weighed to the nearest 0.001 g.

The daily dry matter intake (DDMI) was calculated in two ways.

$$\mathrm{DDMI} = \frac{\mathrm{DFT}}{\frac{\sum_{i=1}^{n} \mathrm{FD}_i}{\mathrm{IRi}}}$$

(1) by calculating the average intake rate from the proportion of food items in the diet and intake rate of separate food items: where DFT=daily feeding time (min), PD_i=proportion in diet of food item i, IR_i=Intake Rate of item i (g min^{-1}).

(2) from the daily dropping production (DDP) and digestibility of the food (only for females during the egg stage):

$$\mathrm{DDMI} = \frac{\mathrm{DDP}}{1 - \sum_{i=1}^{n} D^i * PD_i}$$

where DDP=daily dropping production (g d^{-1}), D_i=fraction digestible of food category i. Food items were categorized into four groups: grass leaves, grass seeds, berries and herbs. Digestibility of herbs could not be determined, instead it was assumed to be similar to grass leaves.

DDP was determined by collecting all droppings produced by females at the nest site. The size of the droppings excluded the possibility of confusion with droppings of the male. After the first large dropping close to the nest, females produced some smaller ones later during the recess. By reconstructing the track of the females using footprints in the sand it was possible on some occasions to check how many additional droppings had been produced while the females were feeding. Dropping productions were corrected accordingly (+20%, *n*=2). Prior to weighing the droppings, all large berry seeds (e.g. Pukiawe) and grit were removed and the sample was dried at 90^{O}C. After weighing, the ash content was determined giving the ash-free dry weight.

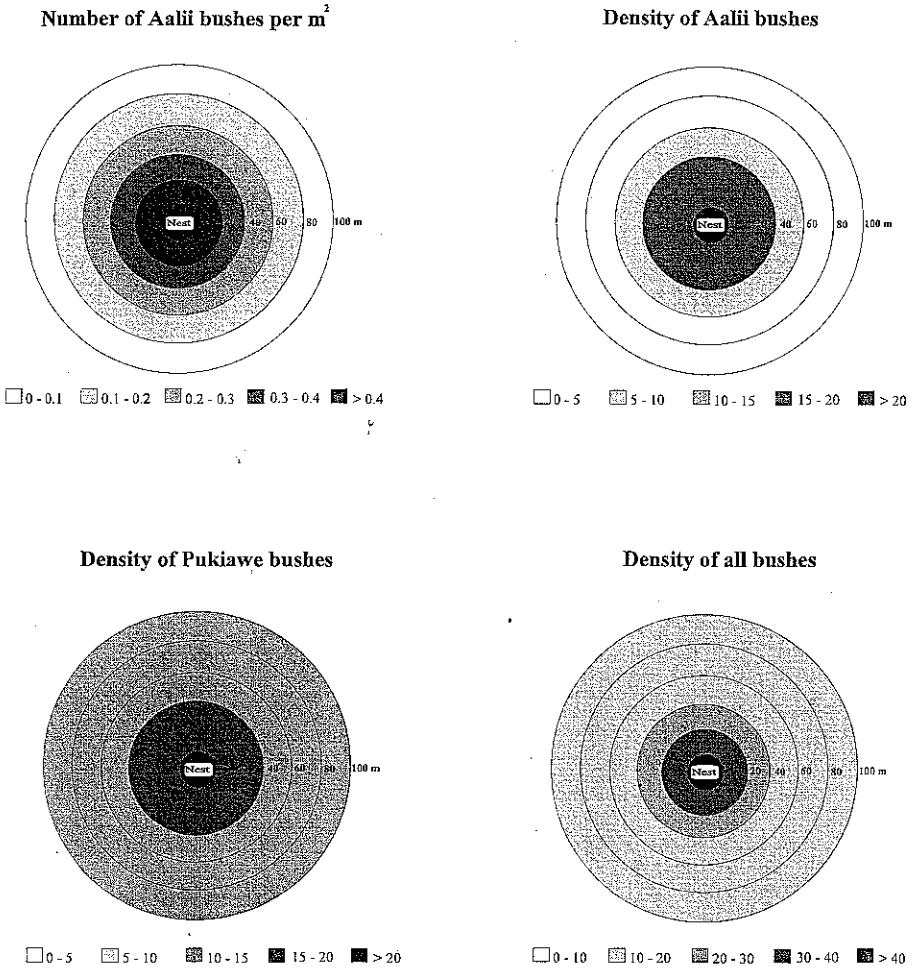


Figure 4. The density of Aalii and Pukiawe bushes in relation to the distance from Nene nest 5.

The energy content (EC) of the food plants was calculated from the chemical composition and caloric values of the components (carbohydrates 17.6 kJ g^{-1}, protein 17.8 kJ g^{-1}, fat 39.3 kJ g^{-1}). The metabolizable energy of the food (ME) was calculated by multiplying the EC by the digestibility, assuming metabolizability was similar to organic matter digestibility (Karasov 1990, JP unpubl.). The daily metabolizable energy intake was calculated as DDMI * ME.

Results

Composition of nesting territories

At Volcanoes, nests were usually located under Ohia lehua trees (eight out of nine cases), occasionally under large Pukiawe bushes (one case). Pukiawe was relatively numerous at all nest sites but Ohelo bushes were numerous only around nest 4. Aalii bushes predominated around nests 1 and 7. Ohia lehua was present in low numbers at all nest sites.

Territories in the Kau Desert at Volcanoes consisted of sparse vegetation which varied in density (about 2 plants per m^2, range 0-16 per m^2, Appendix 1). In some territories the density of the plants was consistent throughout the territory (measured to 100 m circumference), but in others, the area immediately around the nest had most vegetation. For example, Aalii and Molasses Grass *Melinis minutiflora* density decreased with distance away from nest 5 (**Figure 4**) and Pukiawe decreased with dis-

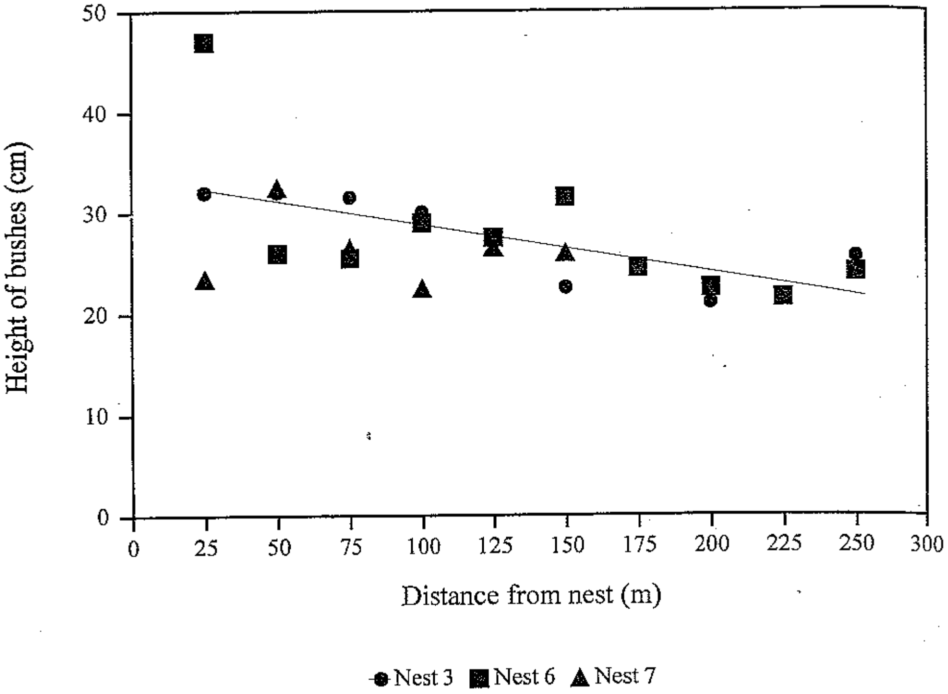


Figure 5. Size of Pukiawe bushes (height) in relation to the distance from a Nene nest. Each symbol represents the average of at least ten measurements. The regression line has been calculated using the original data ($y=32.9-0.044x$, $r^2=0.02$, $n=954$, $P<0.0001$).

tance away from nest 6 (Pearson's correlation tests R=-0.698, $n=30$, $P<0.01$; R=-0.430, $n=30$, $P<0.02$; R=-0.296, $n=46$, $P<0.05$, respectively). There was also some indication that nests were located in the centre of larger bushes (**Figure 5**).

The substrate of the nest territories consisted of volcanic rocks intermingled with sandy patches (nest 1, 2, 3, 6 and 9). One nest was located in a cinder field (nest 4), two others on sand deposits (nest 5 and 8). The area covered by vegetation, especially graminoids, was correlated with the cover of sand in the territory (R=0.222, $n=138$, $P<0.01$). Beardgrass was numerous around nest 1, frequent at nests 3, 6 and 7 but absent from nest sites 4 and 5. Similarly sedge *Bulbostylis capillaris* was numerous around nest 1 but present at only low densities at nest sites 4 and 5. Broomsedge *Andropogon virginicus* was the most numerous plant species at nest site 5 but was present at much lower densities at nest sites 1 and 4. Molasses Grass was present at all nest sites but was most numerous at nests 6 and 7 (see Appendix 1 for complete statistics).

The nesting territories at Haleakala consisted of a well vegetated habitat (about 148 plants per m^2, range 13 - 676 per m^2; Appendix 1). The most abundant species in the territories were Ohelo seedlings, Gosmore *Hypochoeris radicata* and Yorkshire Fog. Some nests were located within 5 m of a grassland such that between 34-83% of the vegetation consisted of Yorkshire Fog grass.

Availability and use of nest sites in the Kau Desert

We estimated the total number of potential nest sites in two large areas in the Kau Desert, where it was most suitable for Nene based on topography and vegetation. We suspect that these areas held the majority of nests in the whole Kau Desert. A total of 56 discrete patches was identified from aerial photographs as potential nesting sites (**Figure 6**). On inspection in the field, 43 of the sites appeared to be inappropriate because no food plants were available in the immediate surroundings. Of the remaining 13 sites, seven were used by nesting geese, or had been used judging by the

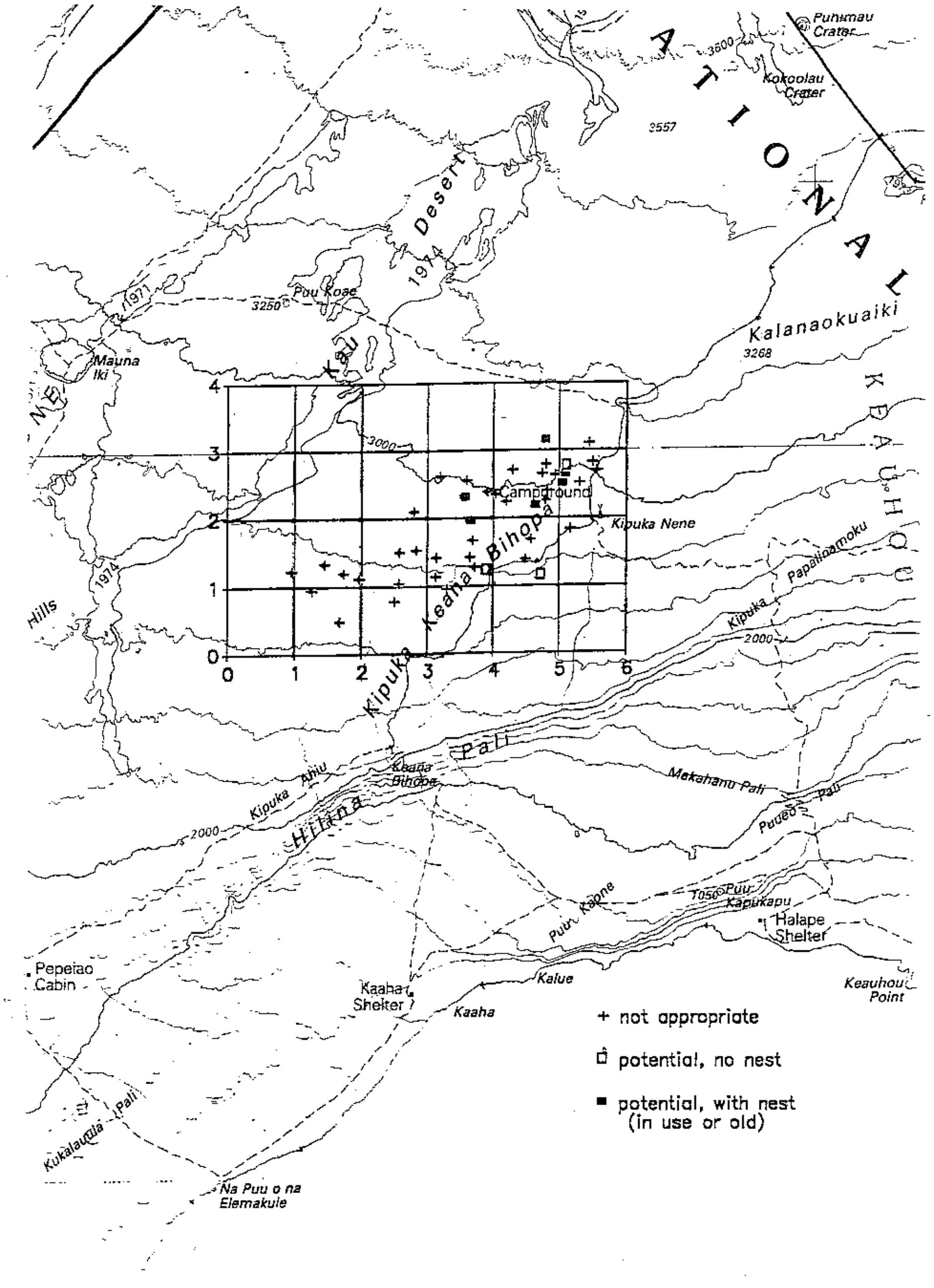


Figure 6. Location of one of the study sites in the Kau Desert which were scanned for Nene nests. Potential nest sites were identified from aerial photographs, and confirmed by ground surveys.

large number of droppings, whereas six were assessed as potential sites without any traces of geese. In additional regions we estimated that 68 ha were potentially suitable for nest sites. Assuming 4 ha as a mean territory size (see below), 17 nests could have occurred in these areas. However, there was evidence of only three nests. So, in total ten out of 30 potential sites were actually used by Nene.

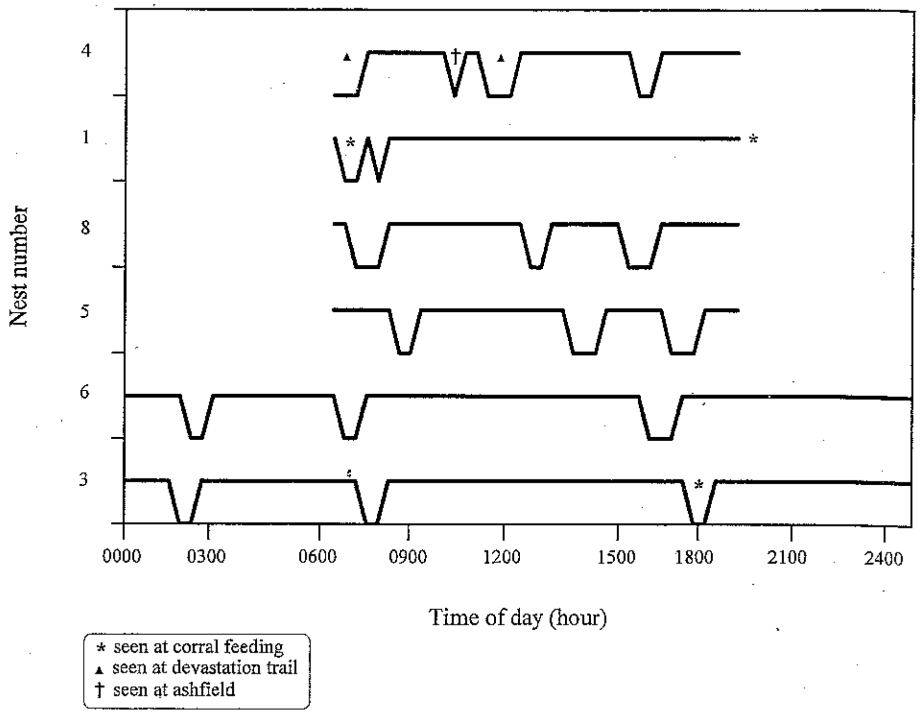


Figure 7. Pattern of incubation recesses by several Nene females (see nest number). The dip in the line denotes time off the nest. The symbols denote the location of foraging bouts during some recesses. The longer lines are from video recordings including night observations.

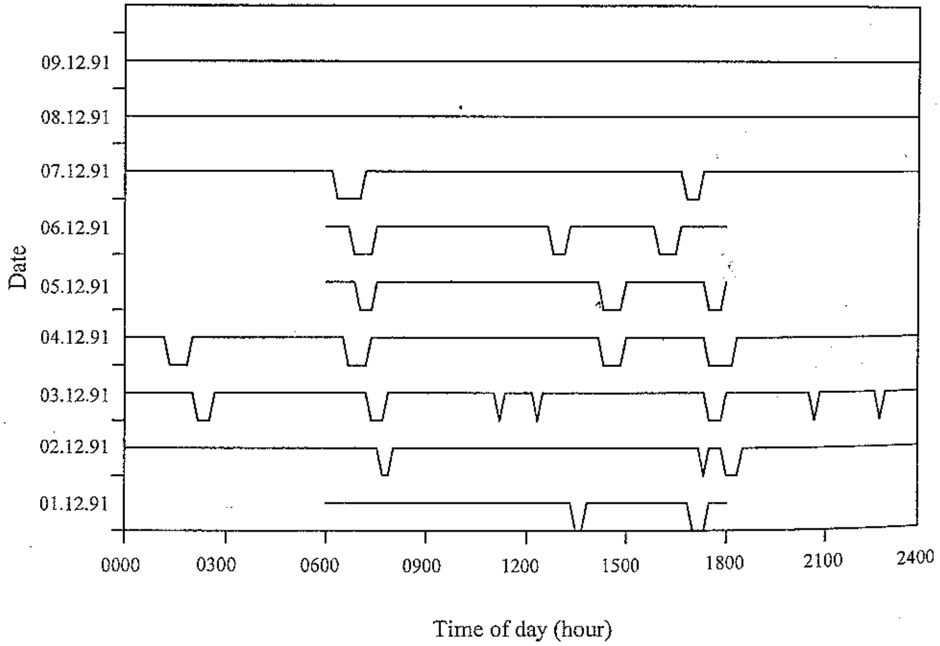


Figure 8. Pattern of incubation recesses by one Nene female. The dip in the line denotes time off the nest. The longer lines are from video recordings including night observations.

Table 2. Time off the nest and feeding time by Nene females during incubation. Percentage time spent feeding is assumed constant for all individuals (44% in the territoriy and 75.7% at pastures).

Nest		1	3	4	6	7	mean
% visits in territory	40	86	15	92	79		
Number of recesses per day	total	2.5	3.25	4.5	2.8	3.9	3.4
	in territory	1.5	2.8	0.7	2.6	3.1	
	off	1	0.5	3.8	0.2	0.8	
Time per recess (min)	total	34	26	32	28	26	
	in territory	31	25	20	27	29	
	off	23	23	33	30	24	
Total time off (min)	total	86	86	143	79	101	99.1
	in territory	47	68	14	69	88	
	off	23	10	127	7	19	
Flying time (min)	total	5.0	2.3	19.1	0.9	3.3	
	in territory	0.0	0.0	0.0	0.0	0.0	
	off	5.0	2.3	19.1	0.9	3.3	
Total time feeding (min)	total	34.5	36.2	87.6	34.9	50.7	48.8
	in territory	20.7	30.1	5.9	30.5	38.6	25.2
	off	13.9	6.0	81.7	4.4	12.1	23.6
	lava	20.7	30.1	87.6	30.5	38.6	41.5
	pasture	13.9	6.0	0.0	4.4	12.1	7.3

Activity patterns during the breeding season

In general, recesses by incubating females were taken at sunrise, sunset, and once or twice during the day or night (**Figure 7**). Within pairs, the daily pattern was relatively constant (**Figure 8**). The average number of recesses per day was 3.4 (SD 0.81, *n*=5 females), of which 0.5 of a recess was taken at night (*n*=2 females with ten complete days, **Table 2**). During 62% of the recesses (SD 33.4, *n*=5) females stayed in the immediate surroundings of the nest. In the other cases, females flew off the nest, usually accompanied by the mate, to feed on grass pastures. One pair (nest 4) was an exception by flying to a cinder field (the Devastation area) where they fed on herbs (Gosmore and *buddleia* sp) rather than on grasses. Flight time between the nesting territories and foraging areas ranged between two and seven minutes. The average time off the nest was 99 minutes (SD 25.9, *n*=5 females).

The intensity with which birds foraged during incubation recesses differed. Females that flew to grass pastures, spent 75.7% (SD 17.4, *n*=4 bouts in 116 minutes) of the time feeding, whereas females that stayed within the nesting territory spent only 44.0% (SD 22.0, *n*=7 bouts in 90 minutes) of the time feeding. The reason for this difference is that pasture feeding geese could feed continuously, whereas the patchy distribution of the food in the territory forced the geese to walk a lot. In the pastures, males fed for only 9.8% of the time (SD 10.9, *n*=4 bouts in 54 minutes), acting as sentinels for the females, compared to 42.3% (SD 28.0, *n*=20 bouts in 462 minutes) when foraging alone in the nesting territory.

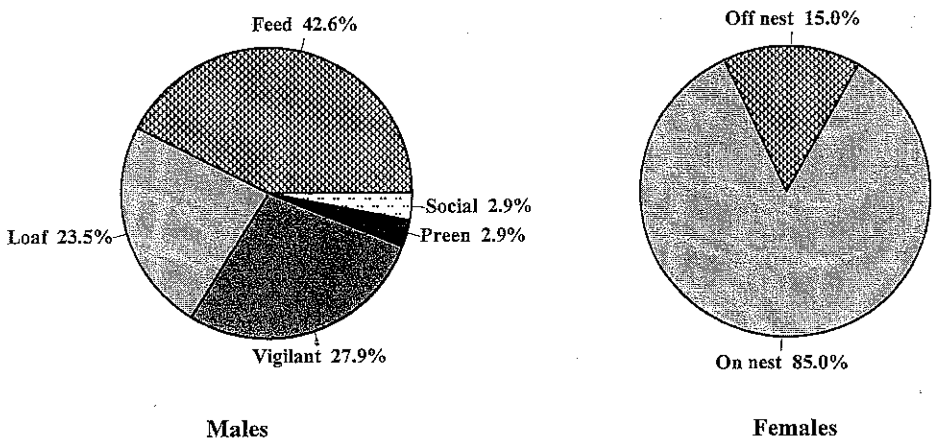
The mean daily feeding time for incubating females was 7.3 minutes on pastures (SD 5.70, *n*=5) and 41.5 minutes on natural vegetation (SD 26.54, *n*=5). The times spent feeding at daylight by males were 2.3 minutes (SD 0.75, *n*=5) and 66.5 minutes respectively. How much time males spent feeding at night is unknown.

At Haleakala, most recesses were spent foraging around the nest which was often within or close to grass pastures (e.g. at Paliku pasture). The average time off the nest by females at daylight was 81.3 minutes (SD 33.52, *n*=4 days), or, assuming a similar night activity as the Volcanoes birds, 93 minutes per day.

Breeding males at Haleakala spent significantly more time feeding than those at Volcanoes ($\neq^2$=166.7, df=1, P<0.001) (**Figure 9**). The feeding time during daylight for male breeders was 281 minutes. The foraging intensity of females was intermediate to the value at Volcanoes; they spent 57.4% (SD 84.9, *n*=74 bouts in 148 minutes) of the 93 minutes off the nest foraging, which means a total of 53.3 minutes feeding per day. Males accompanying their mates spent 32.3% (SD 20.9, *n*=100 bouts in 200 minutes) of the time foraging.

The daily feeding time for birds that were

(i) Haleakala, Paliku



(ii) HAVO

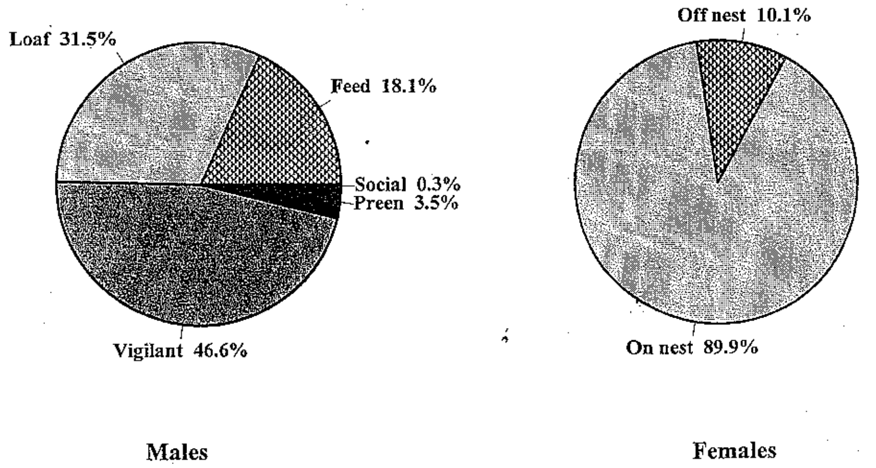
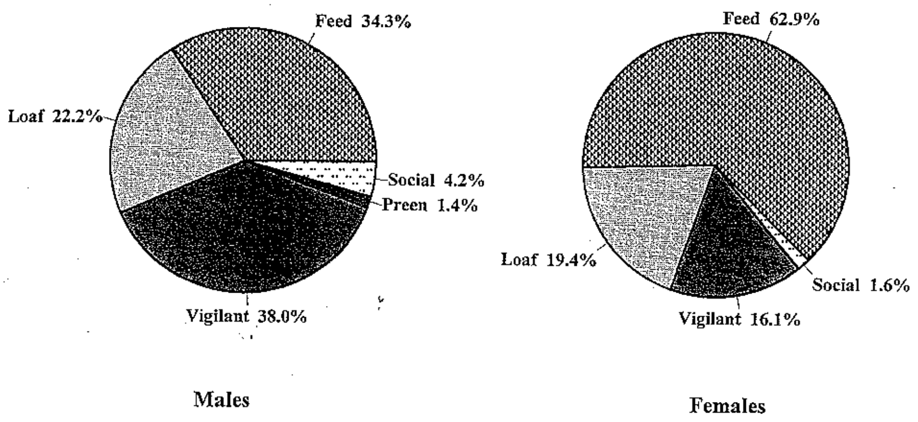


Figure 9. Activity budgets of breeding Nene during incubation at Haleakala and Volcanoes (HAVO) during the breeding season. Based on ten females (2123 records) and ten males (1579 records) in 17 day-hour units.

not attending a nest in the breeding season (non-breeders, failed breeders and pre-breeders) amounted to 240 minutes for females and 157 minutes for males at Volcanoes, and 415 minutes for females and 226 minutes for males at Haleakala (**Figure 10**). At Volcanoes, non-breeding birds were only observed feeding on grass pastures, which means the daily feeding times were underestimated, since from diet analysis (see below) we know they fed on natural vegetation as well.

(ii) Haleakala, Paliku



(ii) HAVO

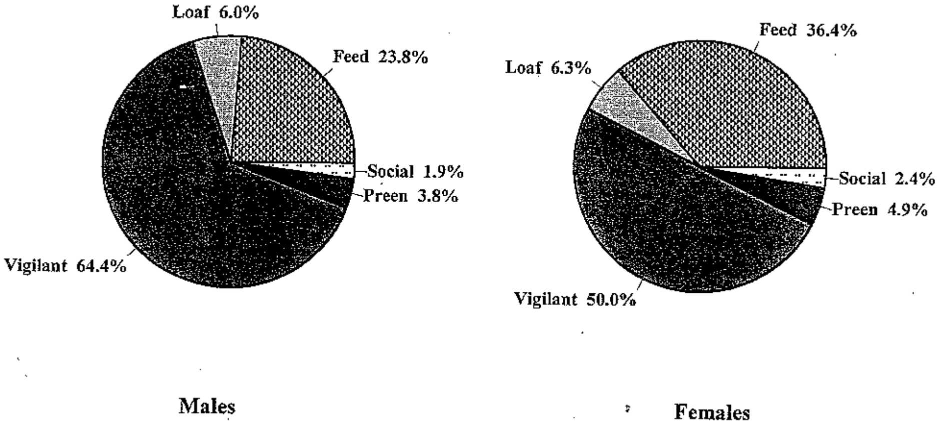


Figure 10. Activity budgets of pre-breeding and non-breeding Nene at Haleakala and Volcanoes (HAVO) during the breeding season. Based on six females (288 records) and five males (316 records).

Feeding activities during the non-breeding season

The average time spent feeding during the 11 hours of daylight varied considerably between sexes and habitats at Haleakala (**Figure 11**). Females always fed more than males. Kuiki birds spent about twice as much time feeding as those at Paliku. This was possibly due to the difference in diet composition; the birds at Kuiki stripped grass seeds, whereas the Paliku birds also fed on grass shoots in the horse pasture and supplementary feed.

The Nene using the extensively managed ranchland on Kauai appeared to rank intermediately between the two Haleakala sites in terms of time spent feeding (**Figure 11**). Long preening sessions occurred at this site in the morning and evening, after bathing in the cattle troughs. Loafing sessions occurred in the middle of the day while the birds sat in the shade. During the heat of the day they were often panting.

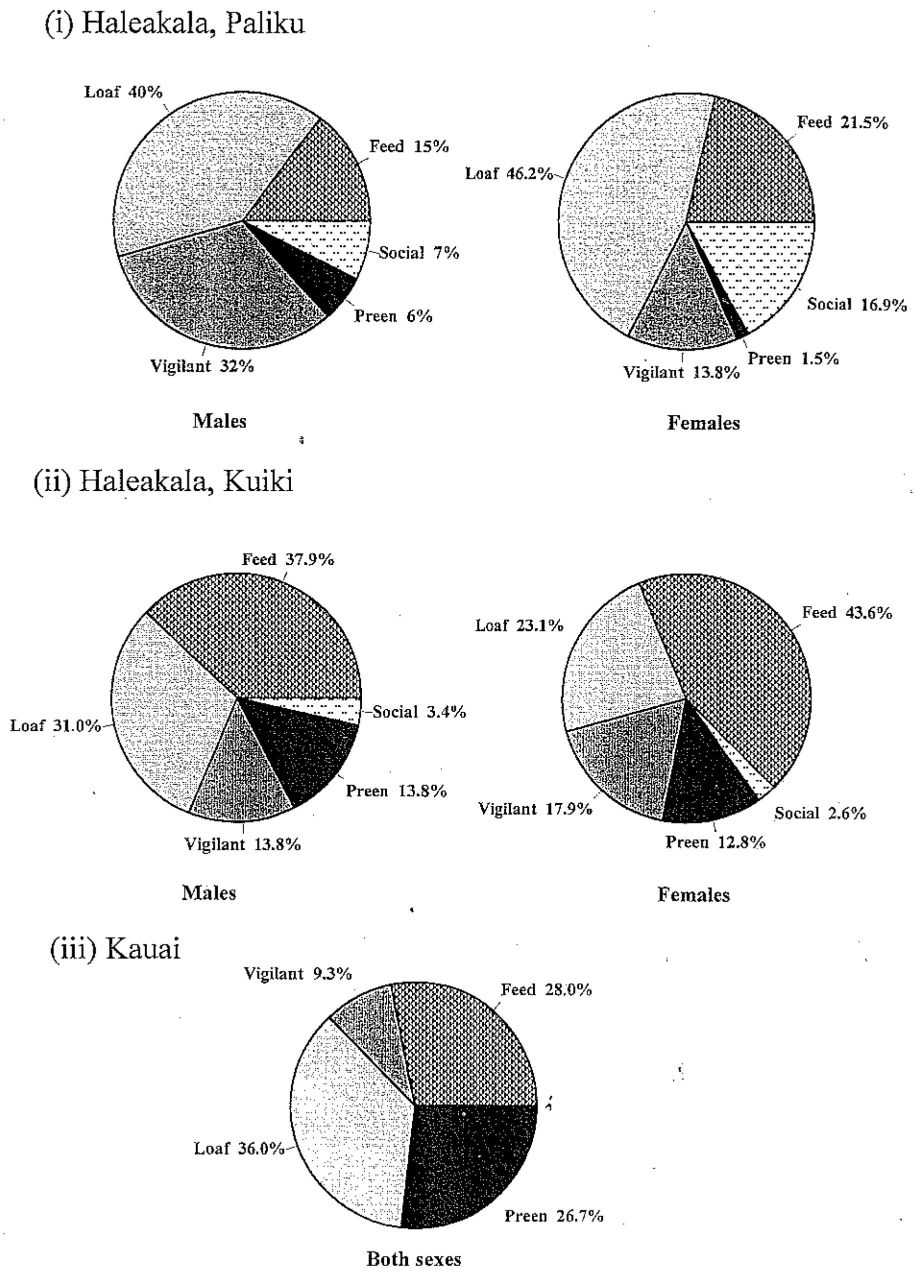


Figure 11. Activity budgets of Nene at two sites in Haleakala and one on Kauai during the non-breeding season. Values were based on daily means of 191 records for 11 females and 12 males at Haleakala and 75 records on 7 unringed birds on Kauai.

Diet

Plant fragments from 247 droppings were identified; 199 from Volcanoes and 48 from Haleakala. From these, 31 plant species were identified including 27 species in the droppings from Volcanoes and 14 from Haleakala (**Tables 3 & 4**). Most of the fragments were of grass leaves and seeds, followed by moderate amounts of berries and

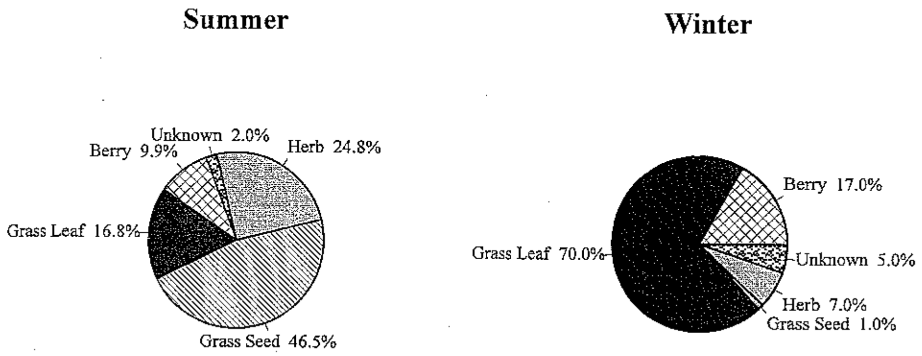


Figure 12. Vegetation types that were eaten by Nene in Haleakala Crater as determined by cell wall fragments in the droppings; grass predominated, followed by berries and herbs. Whereas, grass seeds were stripped in summer, grass leaves were grazed in winter.

fewer herb leaves and flowers (**Figure 12**).

Some grass species could only have been taken from the grass pastures, whereas, most of the other components originated from scrubland habitats. For example, in the droppings of the female at nest 3, i.e. the pair with a complete set of data for the 30 day incubation period, the proportion of berries increased during nesting (Pearson's correlation test R=0.572, n=22, $P < 0.01$). This coincided with fewer visits to pastures as incubation progressed. Figure 13 shows another example of how the diet varied between days; e.g. a berry-only diet one day and a varied diet on another.

Nene ate four different berry species, which occurred in 98.5% of the droppings and making up 36.6% of the overall diet. Pukiawe berries were most prevalent for nearly all bird classes (pre-breeders, non-breeders, breeders during incubation, and parents during brood rearing) at both study sites (Volcanoes and Haleakala). As an indication of how many berries were taken, we counted all the Pukiawe seeds in droppings from four males and four females; a mean of 41 seeds was found in male droppings (SD 43) and 124 seeds in female droppings (SD 78). One bird-class, breeders during incubation at Haleakala, preferred Ohelo berries slightly more than Pukiawe berries (**Table 4**).

Diet, as measured by the abundance of each species, varied in relation to sex, bird-class, area and date (MANOVA range of Wilks' Lambda F values=0.22-0.69, df=30, all P values < 0.001; percentage abundance values were arsine transformed and insignificant interaction terms were removed from the final model). For example, variation in the diet between the sexes was detected for sedge plants, of which females ate more than males (LSM%[1] females 4.6% v males 1.7%), and Broomsedge Grass, of which males ate more than females (LSM% males 4.7% v females 2.0%). Kikuya Grass was eaten in similar amounts by both sexes (LSM% males 4.0%, females 3.0%).

Examples of the variation between bird-classes include Yorkshire Fog Grass, of which non-breeders utilised more than breeders or parents (LSM% non-breeders 37.8%, breeders 19.4%, parents 19.4%), and Pukiawe berries, of which breeding birds ate most and non-breeders least (LSM% breeders 39.6%, parents 28.4%, non-breeders 9.1%). Rattail Grass was taken in similar amounts by all bird-classes (LSM% breeders 3.8%, non-breeders 3.7%, parents 3.2%).

The comparison between areas indicated that, whereas, Haleakala geese fed more on Yorkshire Fog Grass (LSM% Haleakala Nene 57.6% v Volcanoes Nene -6.5%), Volcanoes geese fed more on Pukiawe berries (LSM% Volcanoes Nene 49.8% v Haleakala Nene 1.5%). Hair Grass was utilised at the same level in both areas (LSM% both 2.3%).

Comparisons of different dates showed, for example, that Yorkshire Fog predominated in the winter diet but not the summer

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[1] LSM%=Least Square Means˘100; these values indicate the percentage of the whole diet adjusted for all variables (area, month, sex and bird-class) and differences in sample size. There were a total of 31 species of plant in the diet.

Table 3. Plant fragments found in Volcanoes Nene droppings.

Breeding season - non-breeders - *n* = 8 (winter 1991/92)

Species	Common name	droppings *n*	% droppings	% abundance
Pennisetum clandestinum	Kikuyu Grass	8	100.0	21.6
Andropogon virginicus	Broom Sedge	5	62.5	13.2
Poa sp	Bluegrass	7	87.5	8.5
Festuca megalura	Foxtail Fescue	8	100.0	7.0
Styphelia tameiameiae	Pukiawe	6	75.0	5.7
Schizachyrium condensatum	Beardgrass	7	87.5	5.5
Axonopus fissifolius	Narrow-leaved Carpet Grass	3	37.5	5.5
Trifolium sp	Clover	3	37.5	5.5
Hypochoeris radicata	Gosmore	4	50.0	4.0
Paspalum urvillei	Vasey Grass	3	37.5	3.5
Melinis minutiflora	Molasses Grass	6	75.0	2.5
Paspalum dilatatum	Dallis Grass	3	37.5	2.0
Sporobolus africanus	Rattail Grass	3	37.5	1.0
Holcus lanatus	Yorkshire Fog	3	37.5	0.7
Chamaecrista nictatans	Partridge Pea	2	25.0	0.5
Paspalum conjugatum	Hilo Grass	1	12.5	0.5
Sacciolepis indica	Glenwood Grass	2	25.0	0.5
Dubautia scabra	Naenae	1	12.5	0.2
Unidentified fragments		8	100.0	12.2

Miscellaneous berry pulp (Misc BP) was assumed to be pukiawe and therefore lumped with pukiawe fragments in calculations (Misc BP, *n* droppings = 4, % droppings = 50.0, % abundance = 4.23; pukiawe fragments, *n* droppings = 2, % droppings = 25.0, % abundance = 1.49)

Breeding season - during incubation - *n* = 191 (winter 1991/92)

Species	Common name	droppings *n*	% droppings	% abundance
Styphelia tameiameiae	Pukiawe	190	99.5	51.1
Melinis minutiflora	Molasses Grass	124	64.9	11.5
Hypochoeris radicata	Gosmore	50	26.2	4.9
Andropogon virginicus	Broom Sedge	112	58.6	4.5
Schizachyrium condensatum	Beardgrass	96	42.9	3.6
Bulbostylis capillaris	Sedge	34	17.8	2.9
Trifolium sp	Clover	50	26.2	2.2
Paspalum dilatatum	Dallis Grass	32	16.7	2.1
Pennisetum clandestinum	Kikuyu Grass	39	20.4	1.5
Sacciolepis indica	Glenwood Grass	57	29.8	1.3
Vaccinium reticulatum	Ohelo	20	10.5	1.0
Paspalum conjugatum	Hilo Grass	23	12.0	0.9
Poa sp	Bluegrass	19	9.9	0.7
Sporobolus africanus	Rattail Grass	24	12.6	0.6
Axonopus fissifolius	Narrow-leaved Carpet Grass	15	7.8	0.3
Coprosma ernodeoides	Kukaenene	21	11.0	0.3
Chloris virgata	Finger Grass	22	11.5	0.3
Paspalum urvillei	Vasey Grass	18	9.4	0.2
Chamaecrista nictatans	Partridge Pea	14	7.3	0.2
Coprosma sp	Pilo	7	3.7	0.1
Dubautia scabra	Naenae	8	4.2	0.1
Buddleia sp	Butterfly Bush	5	2.6	0.1
Holcus lanatus	Yorkshire Fog	5	2.6	0.1
Rhynchyletrum repens	Natal Red-top	4	2.1	<0.1
Anthoxanthum odoratum	Sweet Vernal Grass	2	1.0	<0.1
Bidens pilosa	Beggars Tick	2	1.0	<0.1
Unidentified fragments		167	87.4	8.0

Miscellaneous berry pulp (Misc BP) was asumed to be Pukiawe and therefore lumped with 0pukiawe fragments in calculations (Misc BP, *n* droppings=177, % droppings=92.67, % abundance=42.55; Pukiawe fragments, *n* droppings=93, % droppings=48.69, % abundance=8.52)

Table 4. Plant fragments found in Haleakala Nene droppings.

Non-breeding season - *n* = 20 (summer 1992)

Species	Common name	droppings *n*	% droppings	% abundance
Pennisetum clandestinum	Kikuyu Grass	8	100.0	21.6
Holcus lanatus	Yorkshire Fog	17	85.0	31.2
Sporobolus africanus	Rattail Grass	10	50.0	12.4
Hypochoeris radicata	Gosmore	13	65.0	11.1
Deschampsia nubigena	Hair Grass	16	80.0	9.3
Styphelia tameiameiae	Pukiawe	13	65.0	5.3
Pennisetum clandestinum	Kikuyu Grass	9	45.0	4.4
Trifolium sp	Clover	3	15.0	3.8
Vaccinium reticulatum	Ohelo	7	35.0	3.8
Anthoxanthum odoratum	Sweet Vernal Grass	6	30.0	2.5
Festuca sp	Fescue	2	10.0	0.9
Poa pratensis	Kentucky Bluegrass	6	30.0	0.9
Paspalum urvillei	Vasey Brass	2	10.0	0.5
Eragrostis sp	Lovegrass	3	15.0	0.3
Coprosma montana	Pilo	1	5.0	0.1
Unidentified fragments		16	80.0	13.5

Miscellaneous berry pulp (Misc BP) was assumed to be pukiawe and therefore lumped with pukiawe fragments in calculations (Misc BP, *n* droppings = 9, % droppings = 45, % abundance = 3.30; pukiawe, *n* droppings = 9, % droppings = 45, % abundance = 2.04)

Red/brown berry fragments were assumed to be Ohelo and therefore lumped with Ohelo fragments in calculations (Berry, *n* droppings = 6, % droppings = 30, % abundance = 2.81; Ohelo, *n* droppings = 2, % droppings = 10, % abundance = 0.97)

Breeding season - during incubation - *n* = 13 (winter 1992/93)

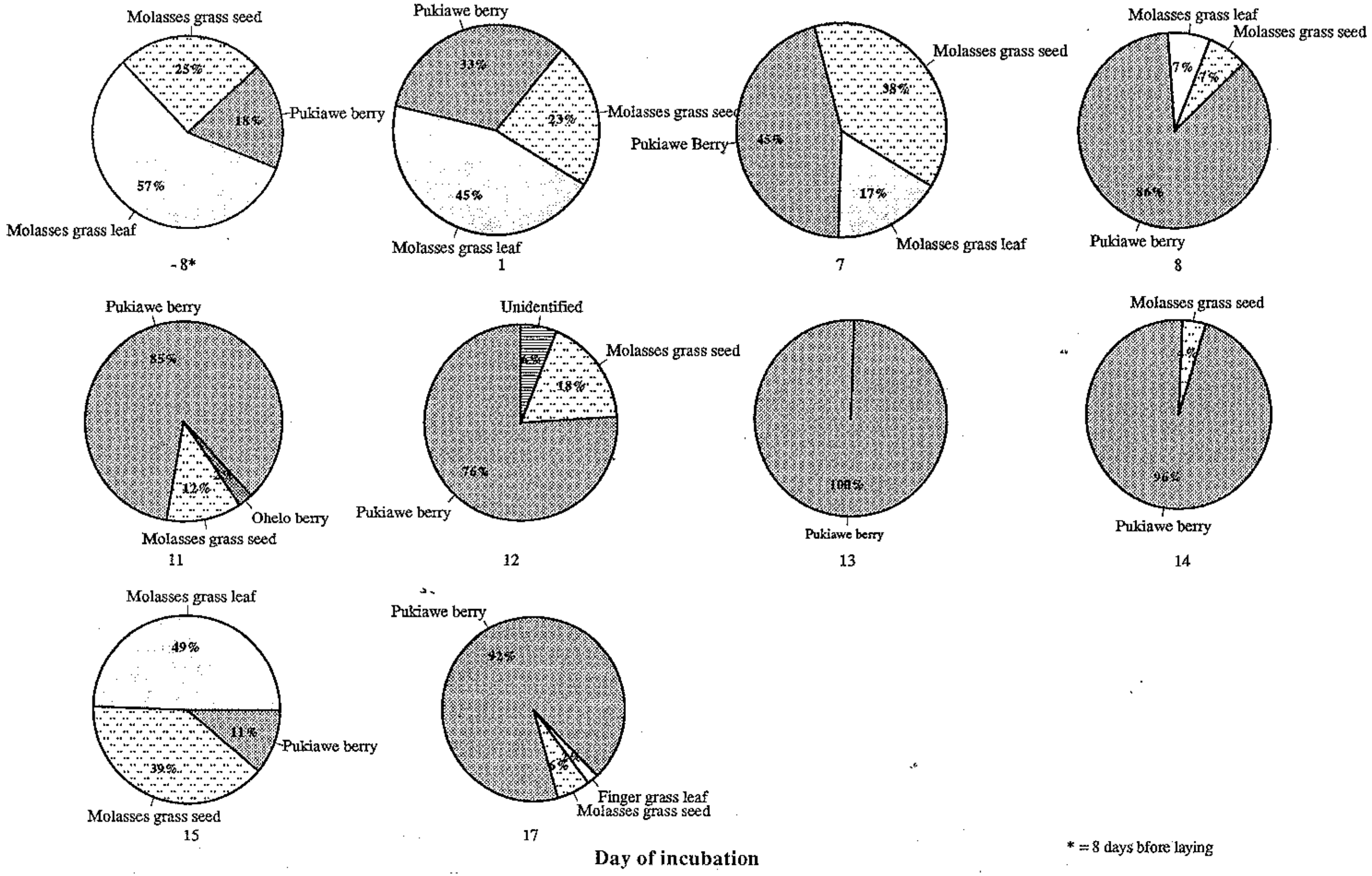
Species	Common Name	droppings *n*	% droppings	% abundance
Holcus lanatus	Yorkshire Fog	13	100.0	51.6
Vaccinium reticulatum	Ohelo	8	61.5	16.3
Hypochoeris radicata	Gosmore	10	76.9	12.8
Styphelia tameiameiae	Pukiawe	7	53.8	8.1
Pennisetum clandestinum	Kikuyu Grass	2	15.4	5.5
Poa pratensis	Kentucky Bluegrass	2	15.4	0.6
Festuca sp	Fescue	1	7.7	0.3
Deschampsia nubigena	Hair Grass	1	7.7	0.1
Trifolium sp	Clover	1	7.7	0.1
Unidentified fragments		9	69.2	4.5

Miscellaneous berry pulp (Misc BP) was assumed to be pukiawe and therefore lumped with pukiawe fragments in calculations (Misc BP, *n* droppings = 6, % droppings = 46, % abundance = 4.33; pukiawe, *n* droppings = 4, % droppings = 30.77, % abundance = 3.74)

Breeding season - non-breeders - *n* = 15 (winter 1992/93)

Species	Common Name	droppings *n*	% droppings	% abundance
Holcus lanatus	Yorkshire Fog	15	100.0	58.1
Pennisetum clandestinum	Kikuyu Grass	12	80.0	11.2
Styphelia tameiameiae	Pukiawe	11	73.3	9.0
Hypochoeris radicata	Gosmore	12	80.0	6.9
Vaccinium reticulatum	Ohelo	3	20.0	6.9
Festuca sp	Fescue	1	6.7	0.8
Poa pratensis	Kentucky Bluegrass	2	13.3	0.4
Deschampsia nubigena	Hair Grass	1	6.7	0.4
Sporobolus africanus	Rattail Grass	1	6.7	0.4
Grain (horse food)		1	6.7	0.1
Unidentified fragments		13	86.7	5.8

Miscellaneous berry pulp (Misc BP) was assumed to be Pukiawe and therefore lumped with Pukiawe fragments in calculations
(Misc BP, *n* droppings = 8, % droppings = 53, % abundance = 4.57; Pukiawe, *n* droppings = 5, % droppings = 33.30, % abundance = 4.44)



* = 8 days bfore laying

Figure 13. Diet composition of nest 6 female over the nesting period.

Figure 14. Per cent abundance of food plants in Nene diet in relation to abundance in their nesting territories, Kau Desert. Top females, bottom males.

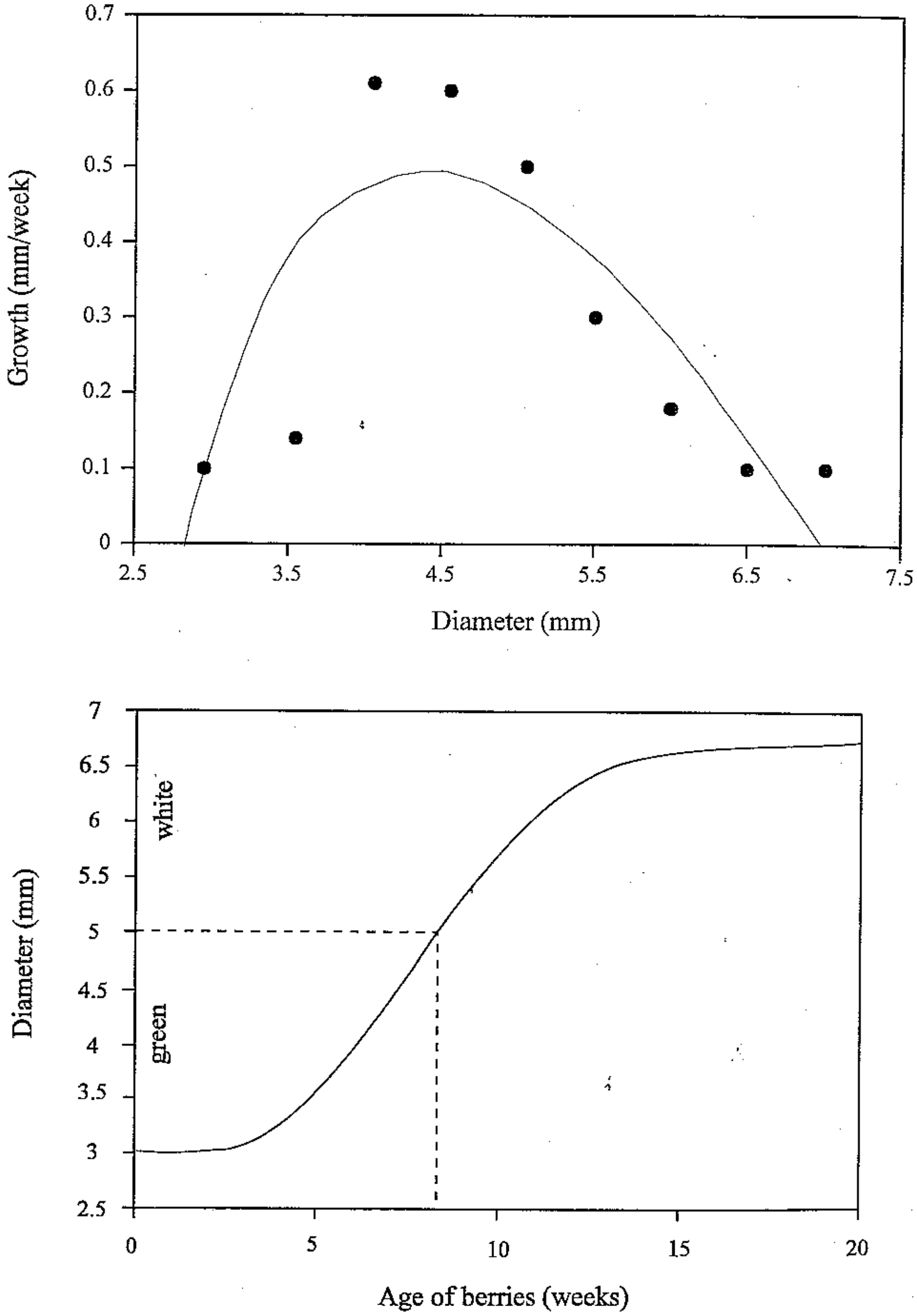


Figure 15. Growth rate of Pukiawe berries in relation to their size (Kau Desert) $y=0.37\check{}0.37/(x-0.47)\check{}(0.84-x)/(x-0.47)\check{}5.31$, N=9, $R^2=0.73$, after log-transformation of diameter). The integral form gives the size of berries in relation to age (bottom).

diet (LSM% -12.0% August, 38.3% November, 38.2% December, 37.7% January), and rattail grass was taken in summer but not in winter (LSM% 13.6% August, 0.1% November, 0% December, 0.5% January). Ohelo berries and Gosmore plants were taken at similar rates throughout the study (LSM% Ohelo (Gosmore) 2.1% (7.5%) Au-

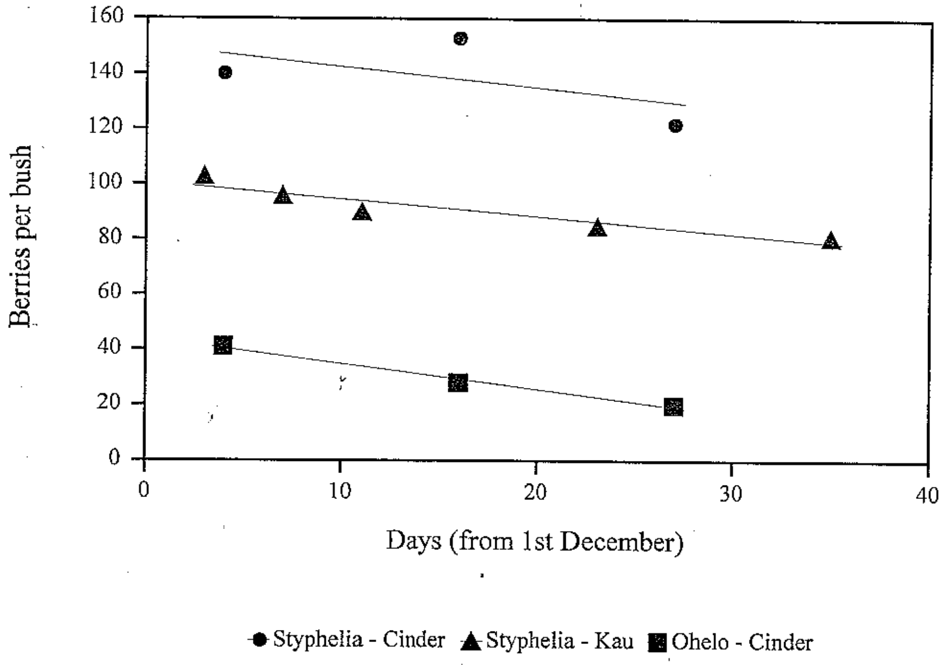


Figure 16. Seasonal trends in the average number of berries per bush for (A) Pukiawe in the Kau Desert ($y=99.7*e^{-0.0063*x}$, $r^2=0.85$, $P<0.01$), (B) Pukiawe at the Cinder field ($y=150.2*e^{-0.0060*x}$, $r^2=0.38$, N.S.), (C) Ohelo in the Cinder field ($y=45.7*e^{-0.033*x}$, $r^2=0.98$, $P<0.01$).

gust, 3.3% (5.8%) November, 5.1% (9.6%) December, 3.2% (7.1%) January).

Diet in relation to food availability

To test whether Nene choose their diet according to the plants that are available in the environment, we compared the percent abundance of items found in the diet with abundances of plant species found in the nesting territories. **Figure 14** shows that relative to their availability, certain foods were preferred (Pukiawe, Ohelo, and Gosmore), some were neglected (Sedge *B. capillaris*, Broomsedge, Beardgrass, Molasses Grass) and others were ignored (e.g. Aalii). Pasture grasses, which did not occur in the territories, were obtained when the geese flew to grassland sites (see *Activity Patterns* above).

Diet and breeding success

Prior to the breeding season at Volcanoes, when pairs were preparing for egg-laying, those that went on to breed had significantly heavier droppings than those that did not (ANOVA F=4.82, *n*=13 subsequent breeders, 24 that did not initiate nests, *P*=0.035). At Haleakala, the diet of successful breeders contained twice the amount of grass leaf compared with failed breeders (Mann-Whitney U test W=20, *n*=five successful, nine unsuccessful breeders,

Table 5. Duration (number of days) of successive phenological stages of berries in different locations (and sample sizes). Unripe: from disappearance of petals to attaining final colour. Ripe: from ripening to shrivelling or falling off.

Pukiawe berries	Kau Desert 28 Nov to 4 Jan	Cinder field 4 Dec to 4 Jan
Unripe	73.6 (91)	44.7 (49)
Ripe	81.1 (217)	79.7 (36)
Ohelo berries	Cinder field 4 Dec to 21 Dec	Cinder field 21 Dec to 4 Jan
Unripe	51.1 (132)	33.6 (144)
Ripe	20.6 (104)	18.8 (47)

Table 6. Rate of production of berries of Pukiawe and Ohelo in different locations as calculated from mortality rate and rate of increase.

	Pukiawe-Kau	Pukiawe-Cinder	Ohelo-Cinder
mortality rate (M)	1.23%	1.25%	5.0%
growth rate (G)	-0.63%	-0.60%	-3.34%
production rate (G+M)	0.60%	0.65%	1.66%

P=0.034). The Volcanoes diet of successful breeders differed from that of unsuccessful breeders by containing more grasses and less herbs (Mann-Whitney U test range of W=4797-6856, *n*=92 successful, 33 unsuccessful, all P values < 0.001).

Availability and production of important food plants

Lava deserts

At the earliest stage of development, the growth rate of Pukiawe berries was low (**Figure 15**). Growth rates peaked when berries reached a size of 4-5 mm. Fully mature berries were 6-7 mm in size. The growth rate in relation to the size of the berries fitted the differential form of a sigmoid growth curve. The growth curve, described by the calculated parameters, is shown in **Figure 15**. The starting point of development was taken as the time when the berries were 3 mm, coinciding with the loss of the petals. **Figure 15** shows that the berries needed eight weeks to develop to an early mature stage, after which they were taken by Nene. An additional four weeks were required for full maturation.

Measurements of the length of successive phenological stages of Pukiawe berries showed an average of 63.5 days for the unripe stage (**Table 5**), which matches with the eight weeks derived from **Figure 15**. Before falling off or shrinking, ripe berries remained on the bushes for an average of 80.9 days. Since berry loss exceeded production of new ones during the period under study (**Table 6**), the number of ripe

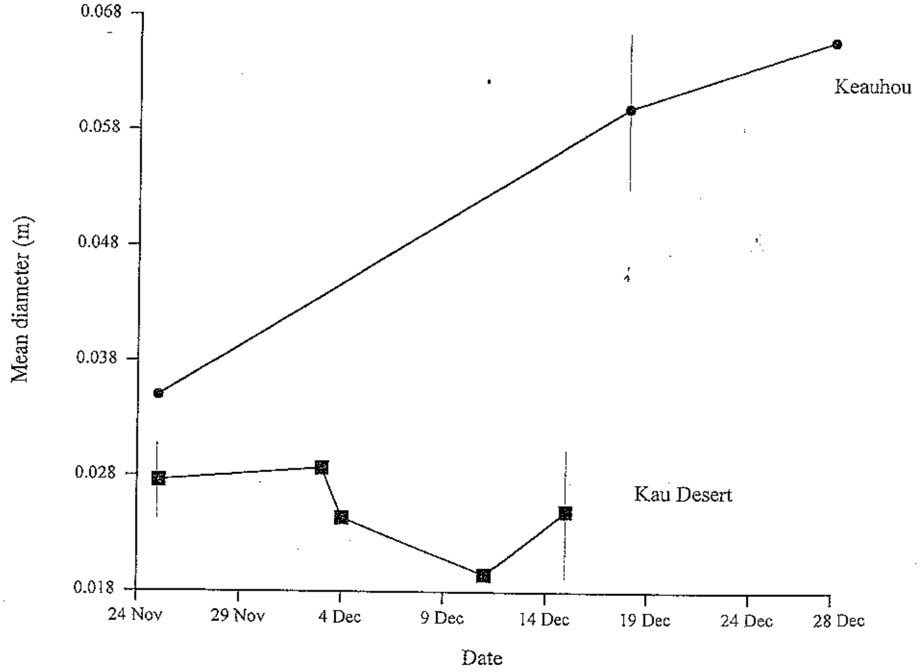


Figure 17. Change in size of Pukiawe berries from two locations over the study period.

Table 7. Density of seedheads at Kapapala Ranch pastures. Values are per m^2.

Topography	Dallis/Hilo grass seeds	Rattail seeds	Carpet grass seeds
Depressions	36.8	8.5	1.9
Gentle slopes	6.8	1.0	5.3
Steep slopes	258.0	3.0	0

berries available on Pukiawe bushes decreased slowly over time (0.63% per day in the Kau, 0.60% per day in the Cinder field) (**Figure 16**).

The number of available Ohelo berries decreased considerably over time (by 3.3% per day) (**Figure 16**). Measurements on the length of successive phenological stages of Ohelo berries showed an average of 42.0 days for the unripe stage (**Table 5**). Ripe (yellow-red) berries stayed for an average of 20.0 days before falling off or shrinking. The production of Ohelo berries was 1.66% per day (**Table 6**).

Comparisons between berry sizes collected at different locations revealed that Pukiawe berries from Keauhou, particularly at the end of the study period, grew to twice the size of those from other areas (**Figure 17**). In other areas, fresh and dry weights of both Pukiawe and Ohelo berries did not change significantly during the study period (ANOVA, $F<2.44$, $P>0.07$, df=4 for all weekly comparisons, $n=36$). Water content was not related to berry size differences between areas.

Beardgrass achieved a growth rate of 3.91 mm d^{-1} shoot^{-1} (SD 2.42, n=47), which was constant over time ($F_{2,44}=0.61$, N.S.). The biomass of green leaves (measured by the total length of leaves per shoot) remained about the same.

Grass pastures

Seedheads were abundant in the pastures at the Kapapala Ranch and Halfway House area, where three types of grass seeds were present: Carpet/Hilo Grass *Paspalum conjugatum*, Rattail Grass and Dallis Grass - listed in the order of abundance (**Table 7**). There were 51.9 seeds per seedhead of carpet and Hilo Grass, 98.1 seeds per seedhead of Car-

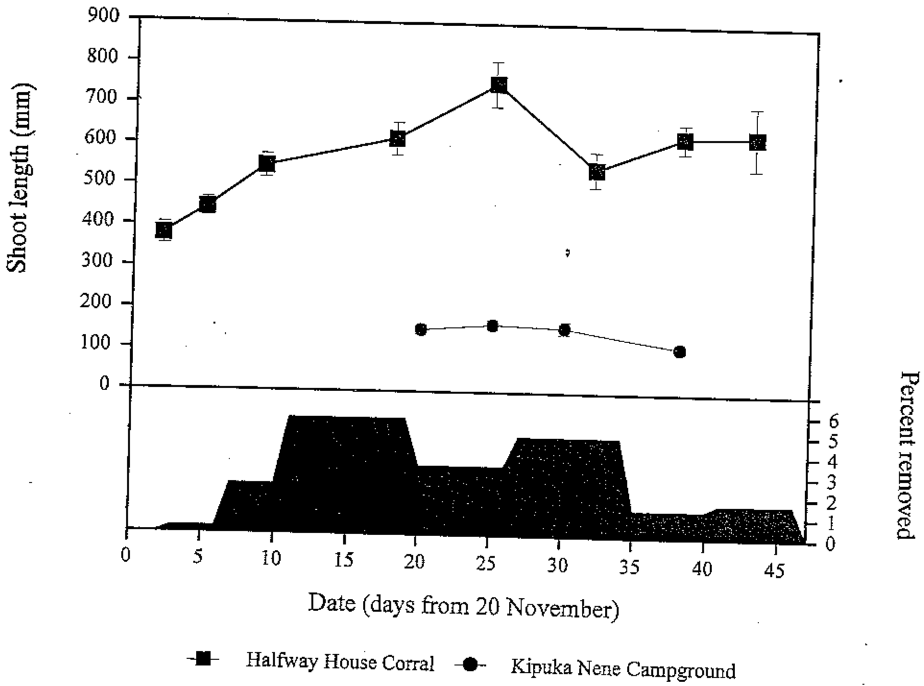


Figure 18. The change insize of Kikuyu Grass leaves throughout the study period at two sites. The lower part of the graph indicates the amount removed by Nene during the intervals.

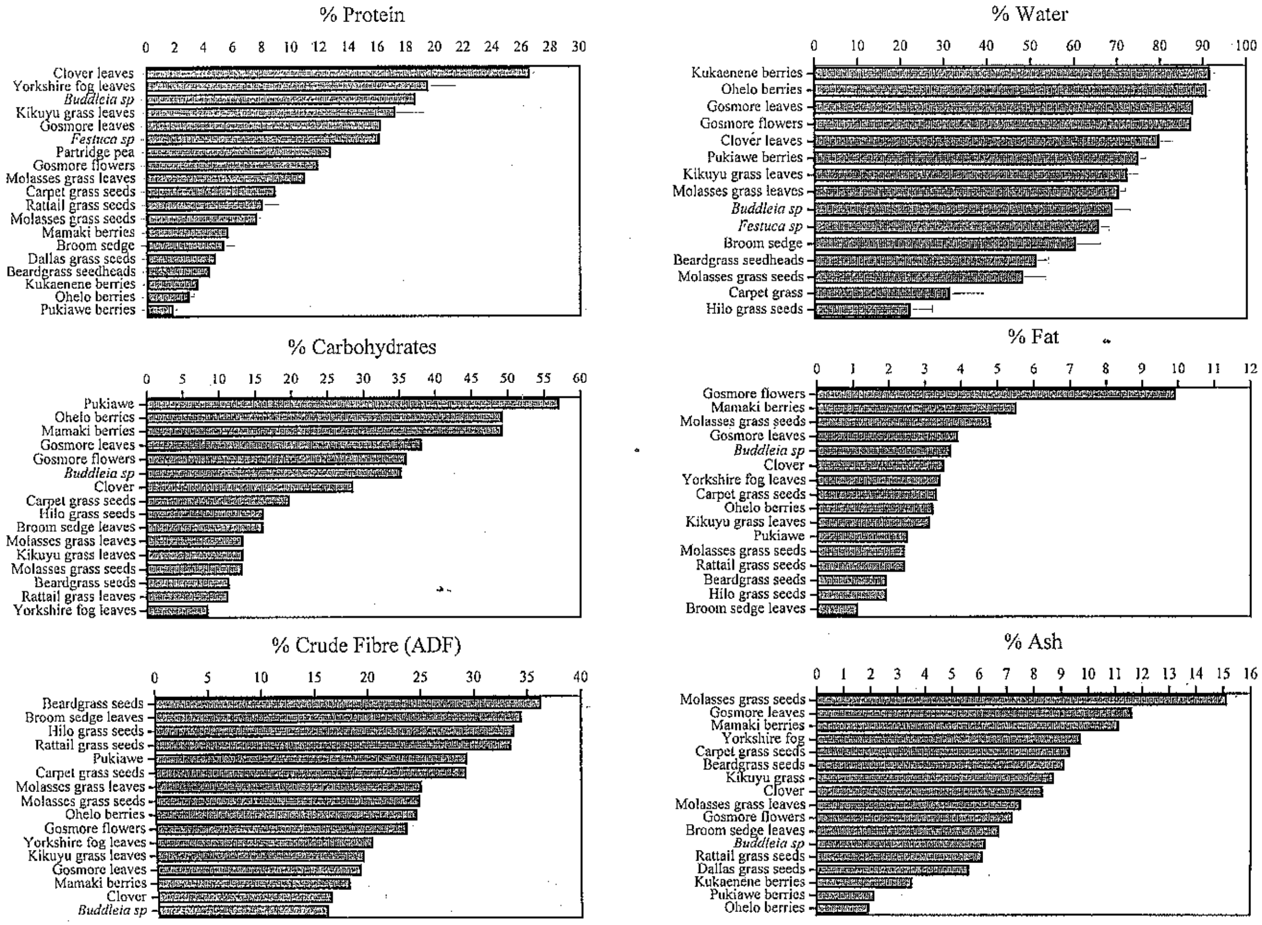


Figure 19. Composition of different Nene food plants. Water content on the basis of fresh weight, all other components on dry weights.

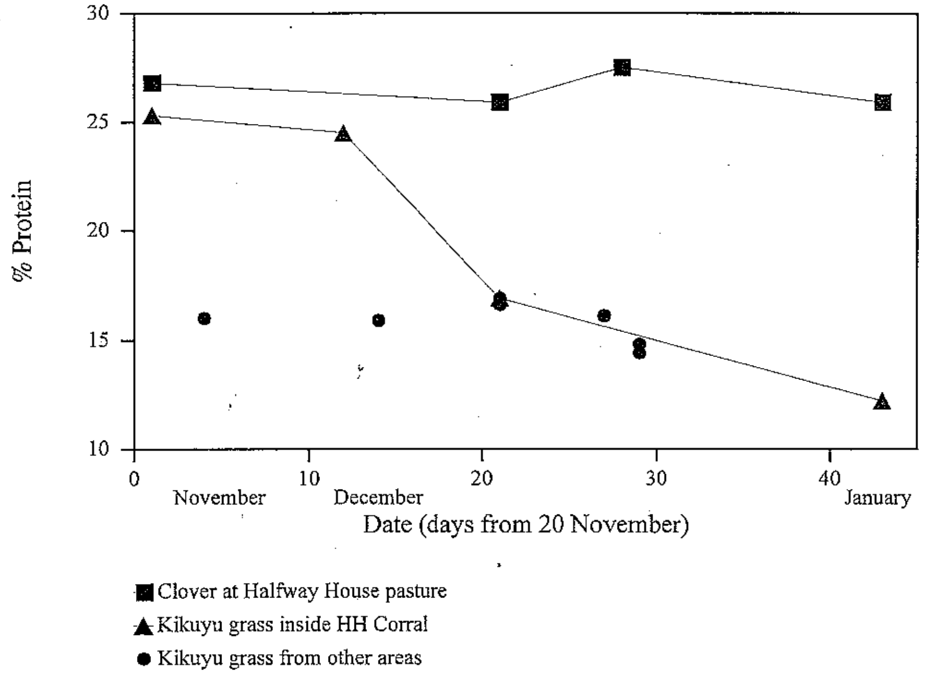


Figure 20. Protein content of Clover and Kikuyu Grass during the study period. The symbols in the legend denote values for Halfway House corral and other areas (including Kipuka Nene Campground, Ainahou Ranch-Volcanoes and the Keauhou Sanctuary pasture).

pet/Hilo Grass, and 559 seeds per head of Rattail Grass. Flowering and production of seedheads of Finger Grass *Chloris virgata*, Rattail Grass and Dallis Grass continued throughout December into early January. The cumulative production of seedheads throughout the study period was 88 m^2 (SD=65.7, *n*=9), which amounts to about three per day.

At Halfway House Corral, Kikuyu Grass increased through mid-December and then stabilized for the remainder of the study (**Figure 18**). From the first week of January 1992, we noticed that the taller plants faded to a yellow colour, which coincided with the presence of grass mites that were feeding on the plants. The lower curve in Figure 18 indicates little growth in the grass at Kipuka Nene Campground.

A comparison of the upper and lower parts of **Figure 18** indicates that the amount of vegetation Nene removed may have been related initially to the growth of new plant tissue. It seems that Nene concentrated grazing efforts on grass that was at its most nutritious phase. The amount removed per day during the growth phase was 4% (SD 1.5), compared to the more stable phase 1.4% (SD 0.3).

Food quality and digestibility

Within grasses, protein is a good measure of the overall quality, since it is correlated with digestibility and energetic value (Tyler 1964, Prop & Vulink 1992). Protein is especially important to goslings (Sedinger & Raveling 1984). Leaves of clover *Trifolium* sp and grasses were ranked as containing more protein than seeds and berries (**Figure 19**). The grasses found in pastures (eg Kikuyu Grass and Yorkshire Fog) were higher in protein than grasses that were found in Nene nesting territories (eg Molasses Grass and Broomsedge). Partridge Pea *Chamaecrista nictatans*, which produces a bean-like fruit, ranked higher than the berries. Clover at Halfway House corral remained high in protein throughout the study, whereas protein in Kikuyu Grass declined (**Figure 20**). Kikuyu Grass achieved the highest protein values (*c* 25%) at the beginning of the study period. Apparently,

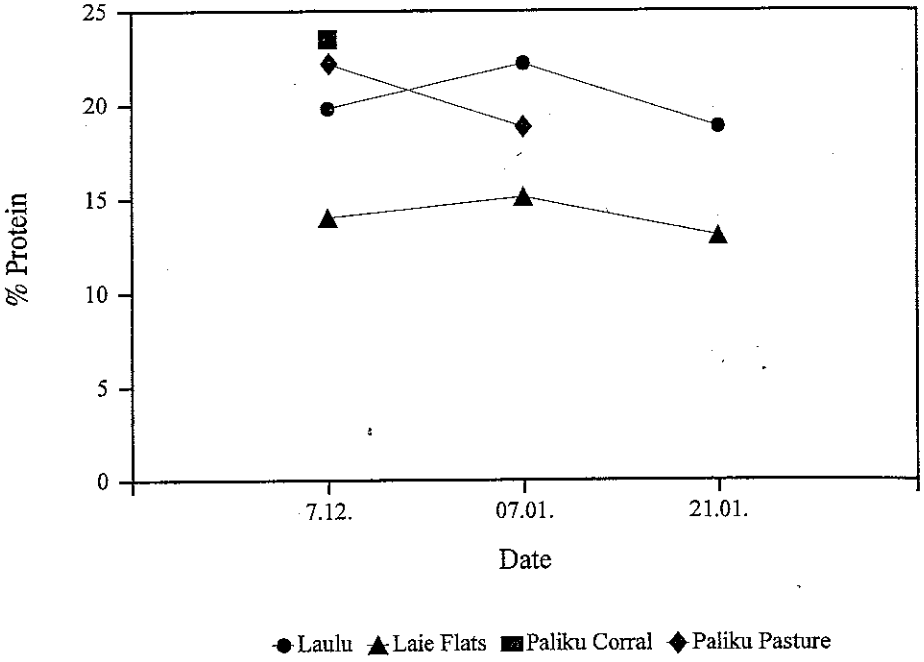


Figure 21. Protein content of Yorkshire Fog at different sites at Haleakala.

just prior to our arrival at the site, the corral had been grazed heavily by cattle (i.e. in early November). Our first measurements, therefore, were during the phase when plants were regenerating new tissue (compare **Figures 18** and **20**); protein content was correlated positively with the length of the grass shoots (Spearman Rank Correlation r_S=1.0, n=4, $P < 0.05$). The kikuyu grass at other sites, including Kipuka Nene Campground, Keauhou Sanctuary paddock and Kahuku pen, had lower protein values (*c* 16%). The lowest value, *c* 12% for Kikuyu grass, was recorded for taller grass at Halfway House pasture (**Figure 20**).

The amount of protein in Yorkshire Fog Grass differed between sites in Haleakala (**Figure 21**). The value from Paliku horse corral ranked highest probably because it had been grazed periodically by horses. Laie Flats ranked the lowest perhaps because of its location - a higher elevation with porous soil.

Berries contained the most water of any food (**Figure 19**). The herbs Gosmore and Clover, ranking second highest for water content, contained more water than grass shoots or seeds. Although Nene have little access to water in some habitats, we think it is unlikely that Nene prefer berries because of the water content as has been suggested by Banko & Manual (1982) since no difference in food choice was observed under sunny conditions or during and after periods of heavy rain fall.

In the Kau Desert, the water content of Pukiawe berries declined over the study period, from 78% (4 December), to 76% (11 December), to 75% (15 December). Percent water content of berries differed among areas, possibly related to differences in phenology. Kahuku had the most succulent

Table 8. Digestibility (% of organic matter) of main food groups of Nene.

Food	ADF (% organic matter) Food	Droppings	Digestibility
Pukiawe berries	34.4	66.3	48.9
Ohelo berries	29.5	8.5	49.6
Rattail Grass leaves	37.3	62.0	39.8
Kikuyu Grass leaves	23.9	32.5	26.5
Yorkshire Fog leaves	24.4	31.8	23.3

Table 9. Composition of the Nene diet as the percentage of pecks per plant species (for males and females separately and all pairs combined).

Sex	Pukiawe Grass seeds	Beard Grass leaves	Beard seeds	Molasses pecks	Ohelo	Naenae	Gosmore	grit	unknown	total
female	79.4	0.1	1.3	0.3	1.4	8.1	0.6	1.2	7.5	909
male	60.8	13.5	1.9	0.6	0.0	0.0	8.6	8.4	6.2	1737

Table 10. Foraging and walking bout length by sex of Nene (as number of pecks or steps and duration) during the nesting period in the Kau Desert. The variance between the sexes was compared by ANOVA. *n* = number of pecks or steps.

	Females			Males			
	Mean	SD	*n*	Mean	SD	*n*	
Foraging							
Pecks per bout	6.99	7.34	130	6.73	7.21	258	NS
Bout length (s)	7.98	8.76	130	14.18	29.68	258	*P*=0.02
Peck rate (*n*/min)	58.47	25.20	126	37.51	20.20	256	*P*<0.001
Walking							
Steps per bout	6.70	7.89	138	4.31	5.58	269	*P*<0.001
Bout length (s)	6.22	7.24	138	7.26	9.38	269	NS
Step rate (*n*/min)	67.42	25.18	133	39.76	16.45	265	*P*<0.001

berries and Kipuka Ainahou had the driest. Volcanoes and Keauhou were intermediate. Pukiawe berries from Kahuku contained 77% water (*n*=3 bags (800 berries)), followed by the Kau Desert (76%, *n*=17 (1700)), Keauhou (73%, *n*=16 (1400) and Kipuka Ainahou (70%, *n*=10 (1000)). Ohelo berries from Kahuku contained 94% water (*n*=2 bags (332 berries)), followed by the Cinder field on Crater Rim, Volcanoes (91%, *n*=1 (212), Keauhou (90.3%, *n*=5 (456) and Kipuka Ainahou (89.8%, *n*=5 (1400)). Kukaenene *Coprosma ernodeoides* berries from Kahuku had 94.3% water (*n*=3 bags (936 berries)), followed by Keauhou (91%, *n*=3 (300)) and Kipuka Ainahou (91%, *n*=11 (1536)).

Figure 19 lists the rank of food items according to the remaining constituent parts. Berries ranked highest in percent carbohydrates, herbs ranked intermediately and grass leaves and seeds were lowest. In terms of the amount of sugar in the various berries, Mamaki *Pipturus* sp ranked highest (38%), followed by Kukaenene (36%), Ohelo (34.9%) and Pukiawe (34.6%). Gosmore flowers had by far the highest percentage of fat, while Broomsedge ranked the lowest. ADF, which is not digestible by geese, ranked highest in Beardgrass and Broomsedge.

Based on ADF as a marker, Pukiawe and Ohelo berries were digested best (**Table 8**), followed by grass seeds. The digestibility of grass leaves was much lower. Given the protein and ADF content, grasses were less digested than plants with similar composition at temperate latitudes (cf Prop & Vulink 1992). This is likely to be caused by tropical grasses containing more digestion inhibitors (Van Soest 1982). Few Pukiawe seeds were digested; out of 76 seeds only ten (13%) of the tough protective coverings were broken. The weight of the seed was 36.4% (seeds from 500 berries) of the total berry weight.

Foraging behaviour and food depletion within nesting territories

From direct observations of breeding birds during the incubation period, we determined that Pukiawe berries were taken more often than other items (79% and 61% of all pecks by females and males, respectively) (**Table 9**). This corresponds well with the analysis of droppings (see **Table 3**).

Foraging bouts were interrupted by short bouts of walking. The foraging bouts of males were longer than those of females (**Table 10**). Because females pecked at a faster rate than males, the number of pecks per bout was similar for both groups.

Walking bout lengths varied from one to 39 steps (**Figure 22**) or, given a step size of 32 cm (SD=8.67, *n*=107), from 0.3 to 12.5 m. To compare this with the distribution pattern of the main food plant (derived from maps like **Figure 3**), the distances (nearest

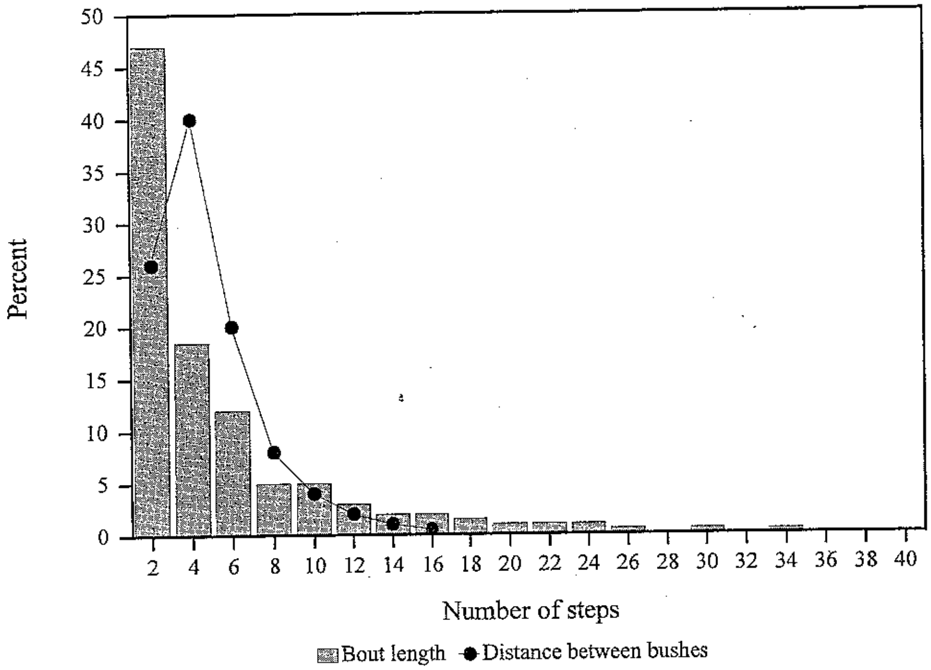


Figure 22. Frequency distribution of walking bout lengths, in comparison with distance between Pukiawe bushes (as multiples of step size).

neighbour) between Pukiawe bushes were expressed in multiples of 32 cm. The frequency distribution of walking bout lengths differed from the pattern of the Pukiawe bushes in a preponderance of very short bouts (1 or 2 steps) and long ones (more than 10 steps) (Kolmogorov-Smirnov 2-sample test, Z=3.29, n_1=526, n_2=408, P<0.005) (**Figure 22**). The short bouts usually occurred when a bird walked around the same bush rather than walking to the next one. The long bouts show that geese may have passed some bushes before selecting a new one. Females stepped at a higher rate than males. The sexes had similar bout durations, so that females made more steps per bout. This suggests that females were more selective in choosing plants on which to feed.

Nene exploited food items at a wide range of levels, from foot level to reaching into bushes up to 65 cm. Females selected Pukiawe berries at a higher level than males (**Figure 23**); sometimes they climbed right into the Pukiawe bushes. Peck rates by males appeared to be lower when foraging at head or above-head level (P<0.05, Scheffe multiple range test). Peck rates by females did not differ among the four levels ($F_{3,374}$=1.51, P=0.20), although rates at above-head-level tended to be reduced in comparison with lower levels. We do not know why females were better able to cope with berries high on the bushes but, perhaps as a consequence of this, they selected larger bushes than males - average height 43.8 cm (SD=25.0, n=29) and 26.4 cm (SD=15.1, n=26), $F_{1,53}$=9.53, P=0.003.

During a single visit to a Pukiawe bush, geese took on average 20% of the berries (**Figure 24**). Bushes were visited several times throughout the incubation period, resulting in a cumulative grazing pressure which was much higher. In particular, the number of berries was severely reduced in the immediate surroundings of the nest (**Figure 25**). By comparing the asymptotic berry densities, the proportion of berries removed (i.e. the maximal grazing pressure) was calculated at 77%, 63% and 60%, respectively for nests 3, 6 and 7. In other words, after the geese had removed about 67% of the berries, they apparently bypassed those depleted bushes in search of more profitable ones. As a result of the heavy grazing pressure, peck rates were re-

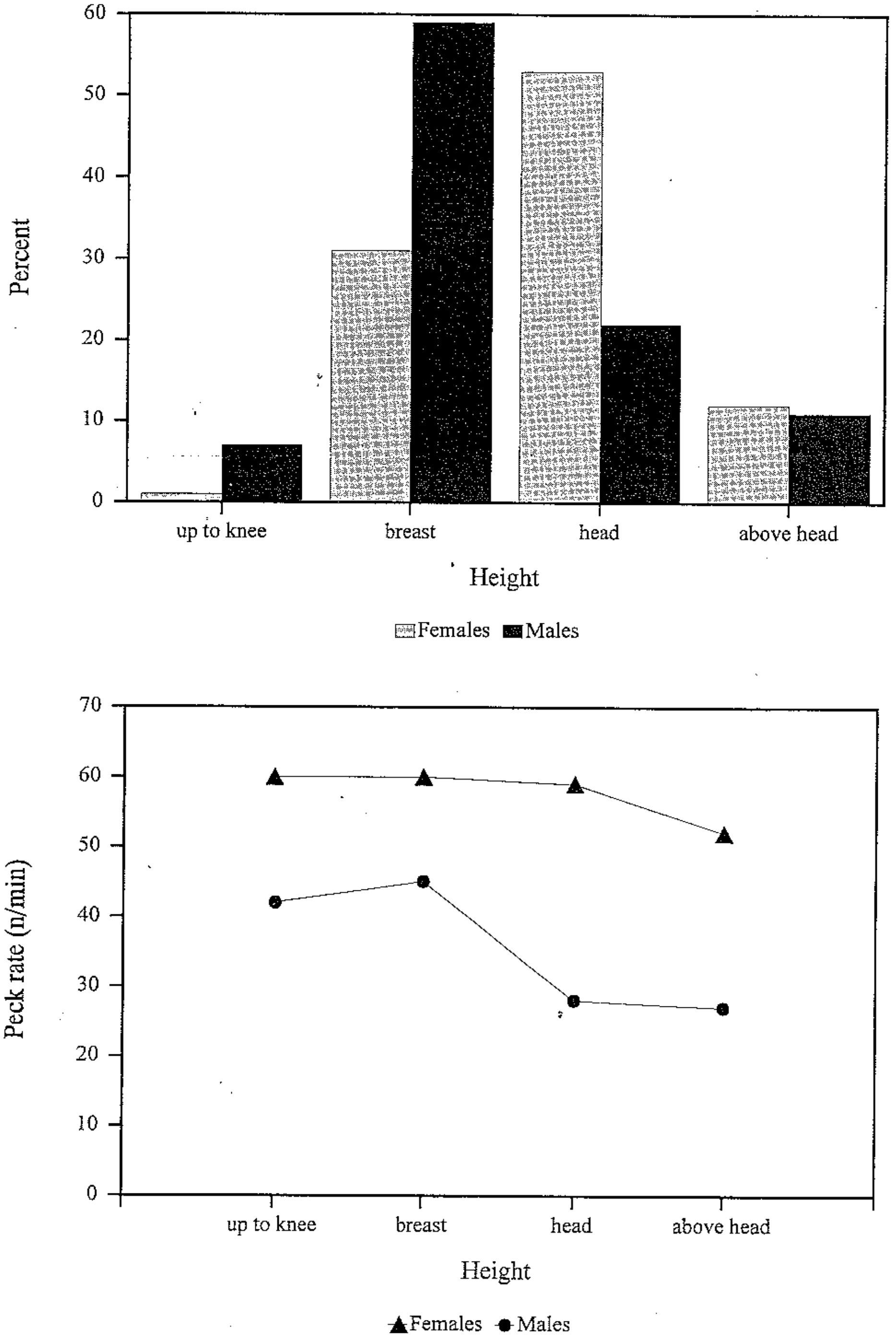


Figure 23. Upper panel. Height of Pukiawe berries when taken by male and female Nenes (as percentage of total number of pecks, n=496 for males, n=378 for females). Lower panel. Peck rates by females and males feeding on Pukiawe berries at different heights.

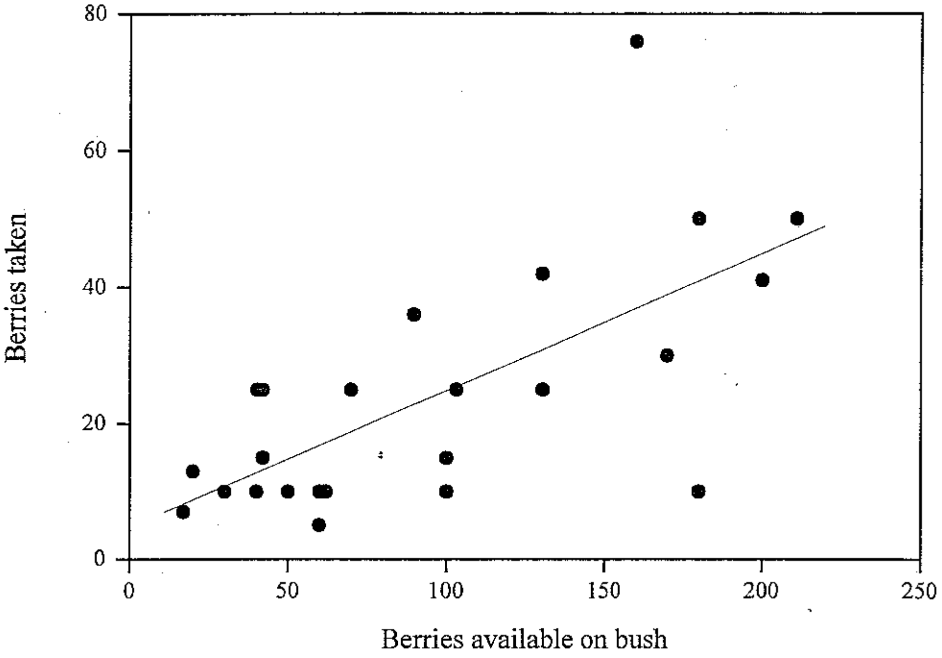


Figure 24. Number of Pukiawe berries taken during a single goose visit in relation to the number of berries available on the bushes (y-4.71+0.20x, r^2=0.48, *P*0.0001).

duced drastically, from over 60 pecks per minute at high-density bushes to 30 pecks at depleted bushes (**Figure 26**). Even within a single feeding bout on a Pukiawe bush, peck rates declined (**Figure 27**). The trends in berry densities at the three nests suggest a lower acceptance threshold of about 2.5 berries per bush (corrected for size), but females appear to be more choosy in ignoring bushes with less than four berries (standardized units) (**Figure 26**). This explains both the longer walking distance between bushes and the higher peck rates by females (**Table 10**).

Food intake & energetics

Figure 28 lists the mean peck rates for Nene foraging on different plant species. Peck rates were highest when feeding on pasture grasses, grass seeds were stripped at a lower rate (e.g. at Haleakala peck rate per min on grass leaves=62.3 (SD 20.1, n=166), stripping rate per min=21.3 (SD 9.5, n=49); (Mann Whitney U test W=3988, $P <$ 0.001). Peck rates on berries were intermediate (Pukiawe) or low (Ohelo). Intake rates, the product of peck rate and bite size, show an almost inverse order (**Figure 29**); food occurring in natural vegetation was ingested at the highest rates, and pasture species at the lowest.

The daily dropping production by females amounted to an average of 22.4 g ash-free (**Table 11**). Given the 39.9% average digestibility of the food of, the daily food intake was 37.3 g. Variation among the four females was small. Calculating daily food intake by multiplying feeding time and intake rate, gave a similar value (37.5 g per day, **Table 12**). The resulting daily energy intake would mean a daily deficit of 705 kJ. Assuming 26 kJ is derived from each g of body reserves (Prop & Deerenberg 1991), females would have lost about 27 g of body mass per day. Incubating females at Haleakala performed similarly. Females incubating in the wild did only slightly worse than captive Nene at Slimbridge, where food is plentiful (**Figure 30**: average weight loss for three successful females was 22 g day^{-1}). Males achieved a higher energy intake during incubation than females, although males at Volcanoes apparently lost weight as well.

Observations indicate that non-breeders feeding at the Halfway House and Kapapala pastures at Volcanoes did not ingest suffi-

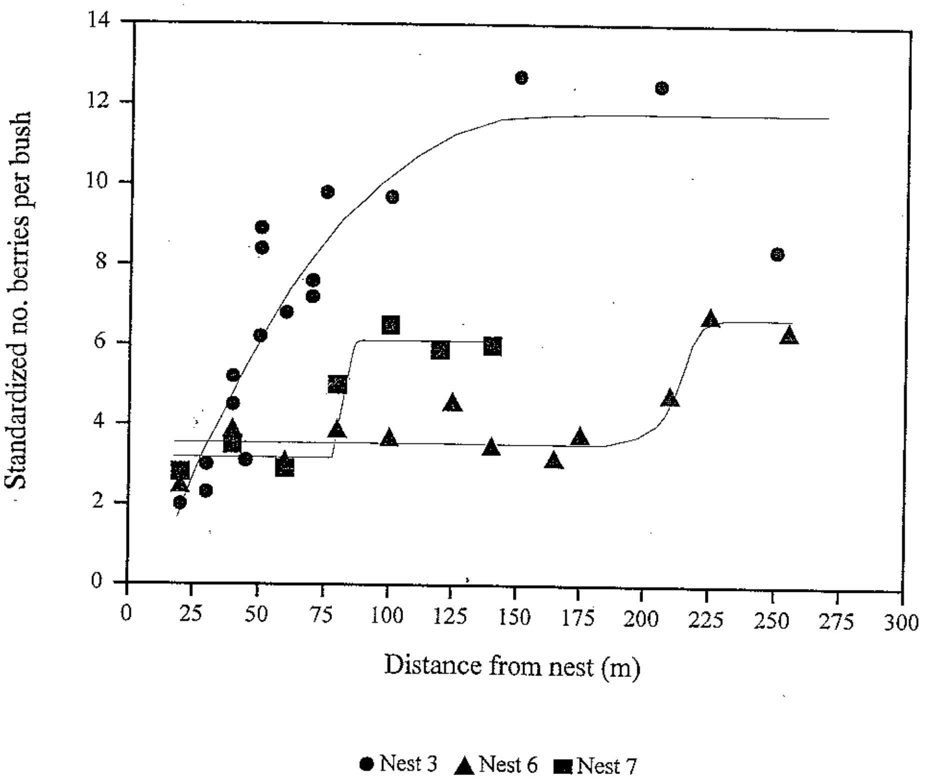


Figure 25. Number of Pukiawe berries per bush (corrected for the size of the bush) in relation to the distance from the nest. Nene pair #3 nested in the western kau Desert, pairs #6 and #7 in the eastern part. Sigmoid curves were calculated by non-linear regression to fit $y=a+b/1+e^{-e(x-d)}$.

cient food to maintain constant body mass (**Table 12**); females may have lost as much as 22 g day^{-1}. However, the diet analysis showed that these birds were feeding on natural vegetation as well (see above). This means the energy intake of non-breeders was underestimated to some extent. By comparison, Haleakala females may have gained as much as 30 g day^{-1}.

Discussion

Breeding success and food supply

During incubation, geese obtain part of the energy requirements by feeding; the remaining amount is derived from body reserves (Ankney 1984). Comparison among northern breeding goose species shows that larger geese are able to deposit relatively larger body reserves (Ankney 1984). As a consequence, the time spent off the nest for feeding is inversely related to body mass (Thompson & Raveling 1987). The intermediate-sized, tropical Nene appears to fit well within this trend (**Figure 31**). Nene derived most food from natural vegetation on lava flows and volcanic deposits. Apparently this habitat provides favourable foraging conditions, as the daily energy deficit during incubation for wild Nene was just slightly higher compared to captive birds which were provisioned with an abundant food supply (compare **Table 12** and **Figure 30**). In energetic terms, there seems to be no barrier to successful breeding for wild Nene. Indeed, during our study at Volcanoes one of the two pairs that were unsuccessful, gave up after incubating a clutch of infertile eggs for a period of 43 days (i.e. 13 days longer than required for hatching. However, we observed a seasonal decline in food quality and density, i.e. a decreasing protein content in grasses (**Figure 20**), a decline in density of grass seedheads and a decline in water content and density of berries (**Figure 16**). It is likely that this sea-

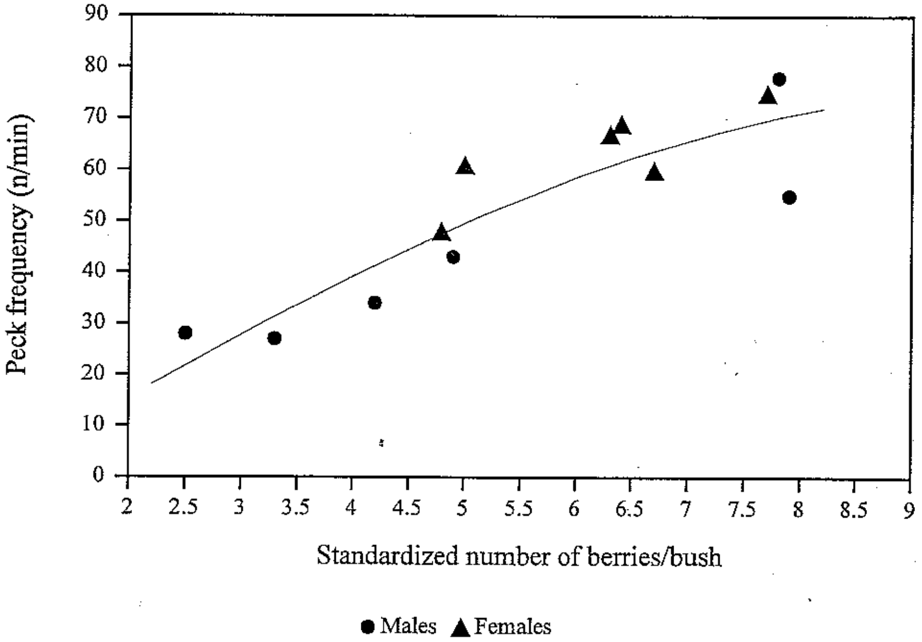


Figure 26. Nene peck rates in relation to the number of berries per Pukiawe bush (corrected for size). The line combines data for males and females ($y=100.94*(1-e^{(-(x-1.28)/(5.40))})$, $r^2=0.80$, $n=12$).

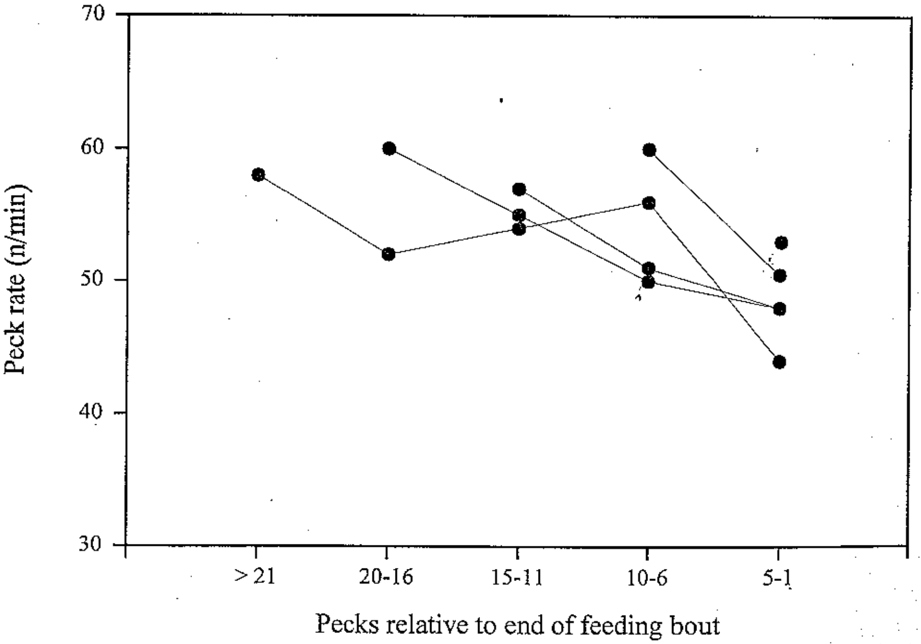


Figure 27. Peck rates of Nene feeding on Pukiawe berries declined towards the end of a foraging bout. Data for different bout lengths are given separately. Analysis of covariance $F_{1,228}=7.92$, $P=0.005$, after adjusting for bout length effects.

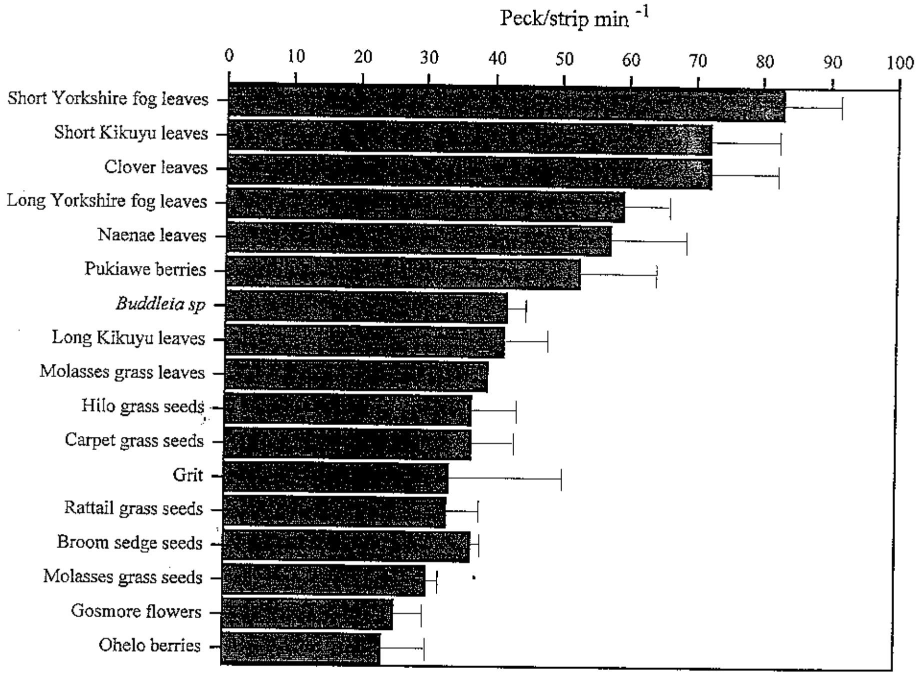


Figure 28. Peck rates on different food items by Nene.

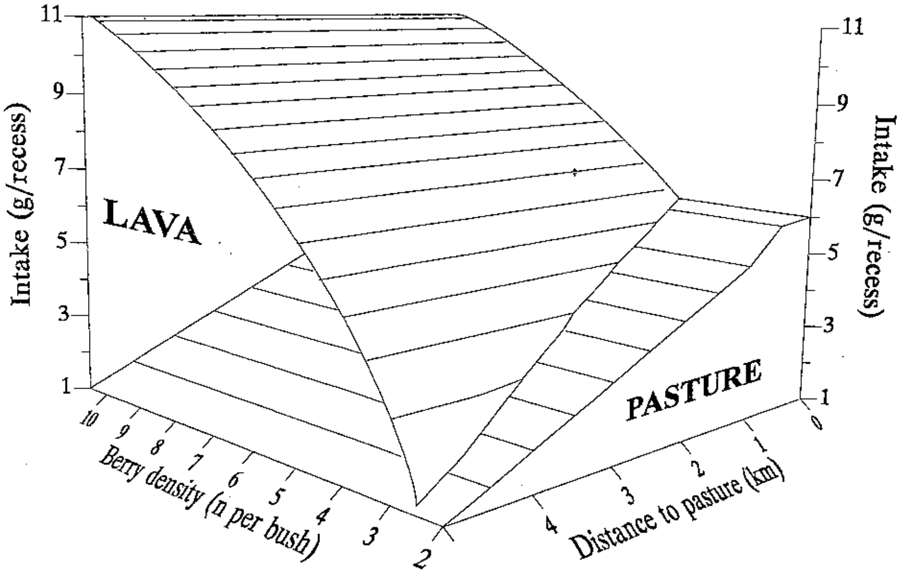


Figure 29. Intake of food per Nene recess in the lava desert depends on berry density (see also Figure 24), and distance to pastures, i.e. the flight time. For this calculation, recess time was taken as constant at 25 minutes.

Table 11. Daily dropping production, digestibility of food, and daily food intake for four Nene females during incubation.

Nest	days *n*	Dropping production (g per day, ash-free)	Digestibility of food (g per day)	Intake
3	4	21.0	40.0	34.9
4	4	24.8	38.4	40.3
6	15	21.1	41.3	36.0
7	10	22.8	39.9	37.9
Mean		22.4	39.9	37.3

Table 12. Daily dry matter and energy intake of Nene by sex and breeding status. Values for non-breeders and breeding males are excluding night feeding.

Social class	Time foraging (min)	Dry matter intake (g)	Energy intake (KJ)	Surplus/deficit (kJ)
Volcanoes breeders				
Females	48	37.5	295	-705
Males	119	97	756	-324
Haleakala breeders				
Females	53	54	302	-698
Males	281	283	1585	+505
Volcanoes non-breeders				
Females	240	72	418	-582
Males	157	47	273	-807
Haleakala non-breeders				
Females	415	417	1835	+835
Males	226	227	999	-81

sonal pattern restricts the period that geese have available for breeding, just as the spring flush of plant growth delimits the time for reproduction in arctic-breeding geese (Owen 1980a, Sedinger & Raveling 1984, Owen & Black 1989, Prop & de Vries 1993).

On a local scale, climatic conditions on the mountain slopes of Hawaii vary greatly, and may depend on volcanic activity (Armstrong 1983). This probably affects the phenology of berry bushes and other food plants for Nene, so that the period appropriate for breeding varies across micro-climates. For example, within the 35 km long study area at Volcanoes we often wit-

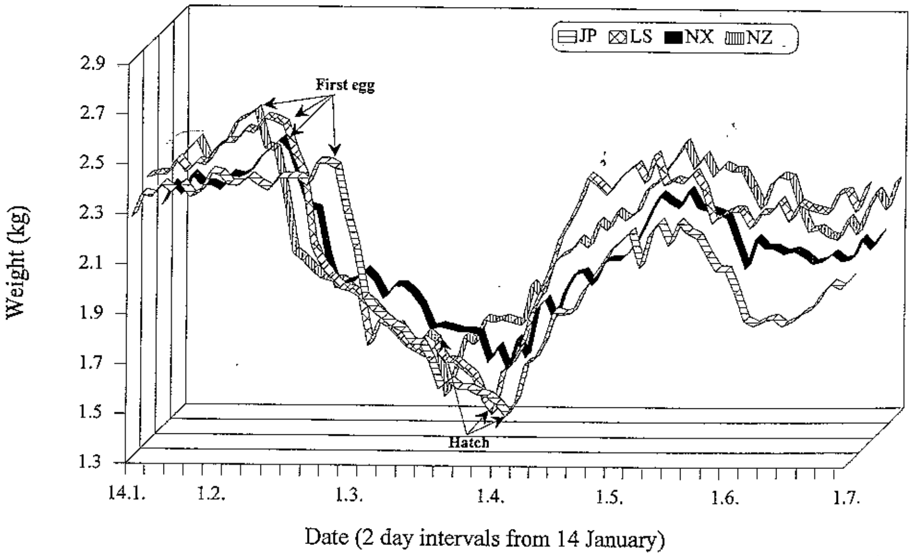


Figure 30. Weight loss of female Nene during incubation at Slimbridge.

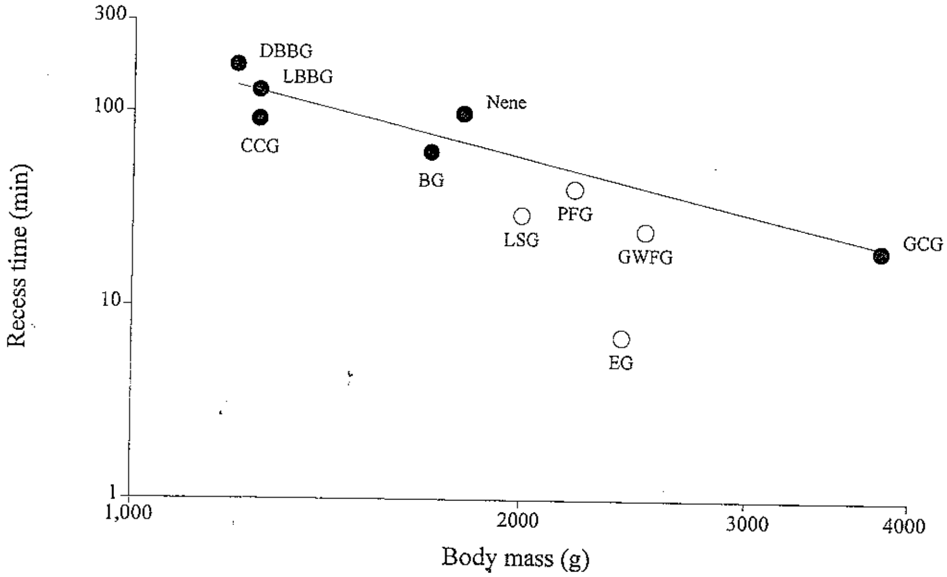


Figure 31. Average time off the nest per day by female Nene during the incubation period in relation to bodymass during the non-breeding season. The regression line is for Branta species only. GWFG - Greenland White-fronted Goose *Anser albifrons flavirostris* (Stroud 1981); PFG - Pink-footed Goose *A. brachyrhynchus* (Knglis 1977); LSG - Lesser Snow Goose *A. c. caerulescens* (Harvey 1971); GCG - Giant Canada Goose *Branta canadensis maxima* (Cooper 1978); CCG - Cackling Canada Goose *B. c. minima*; DBBG - Dark-bellied Brent Goose *B. b. bernicla* (Spasans et al. 1993); LBBG Light-bellied Brent Goose - *B. h. hrota* (Madsen et al. 1989); BG - Barnacle Goose *B. leucopsis* (Prop & De Vries 1992); EG - Emperor Goose *A. canagicus*; Nene *B. sandvicensis* (this study).

nessed a range of weather systems when travelling to different nest sites, e.g. prolonged dry conditions, prevailing heavy mist and rain. Variation in breeding success within and between sub-populations of Nene, therefore, is probably determined by local climate and subsequent plant phenology.

In most years, some of the upper montane areas are probably too dry for breeding, even when artificial foods are offered to Nene (e.g. Keauhou Sanctuary, and Puu 6677, Banko & Elder 1990). The fact that released birds abandoned these areas for more humid areas (grass pastures) confirms our impression (Black *et al.* 1993, Rojek pers comm). The fact that these geese, which have captive backgrounds, lack traditional movement patterns between sites may mean they have limited knowledge of a number of habitats and, hence, limited opportunity to improve on poor local conditions. This lack of cultural tradition was thought to be a major reason for the high mortality and low productivity of released Nene in the highlands during periods of prolonged drought (see Black *et al.* 1993).

Food depletion and territory size

We have shown that female Nene are more selective than males. They utilise larger bushes with a higher density of berries. Due to the slow regrowth of berries, bushes are harvested once per season. As the incubation period continues, the geese have to travel further distances to find adequate food. Females probably travel the greatest distances from the nest in order to maximise intake rates - a peck rate of >50 min^{-1} on bushes with a berry density of >5 (**Figure 29**). As a consequence females walk faster (i.e. almost at a run) for longer periods of time and reach further into the bushes to acquire berries. For three nests (**Figure 25**), females had to move on average 105 m from the nest to maintain this intake rate. Assuming the Nene's territory is circular, we arrive at a requirement of 4 ha per nesting territory. The ultimate size of the territory may also depend on the availability of alternative food sources (e.g. pastures at variable distances).

The Nene at Volcanoes appear to choose nest sites based on a gradient in bush density and size, including dense cover for the

Table 13. Diets of several goose species[1] in comparison with Hawaiian Geese (this study). The asterisks indicate diets consisting of agricultural plant species; 86% of the goose diets in the non-breeding season consist of human cultivated (agricultural) plants.

Goose species	Primary food type	Plants in diet	Reference
Non-breeding season			
White-fronted	grass shoots*	9	Owen (1971)
Barnacle	grass shoots*	13	Owen & Kerbes (1971); Ebbinge *et al.* (1975)
Canada (eastern)	corn grain*	6	McLandress & Raveling (1981)
Canada (western)	*zostera* shoots & grass shoots	9	Buchsbaum & Valiela (1987)
Lesser Snow	grass shoots*, tubers & corn grain*	7+	Alisauskas *et al.* (1988)
Hawaiian (Haleakala)	grass seeds*	17	this study
Pre-breeding season			
Canada	grass shoots*	8	McLandress & Raveling (1981)
Greater Snow	grass shoots* & marsh plant rhizomes	14	Bedard & Gauthier (1988)
Pink-footed	grass shoots*	5	Madsen (1985a)
Barnacle	grass shoots*	7+	Black *et al.* (1991)
Lesser Snow	corn grain & grass shoots	8+	Alisauskas & Ankney (1992)
White-fronted	grass shoots & bulbs	5	Budeau *et al.* (1991)
Hawaiian (Volcanoes)	grass shoots*	20	this study
Hawaiian (Haleakala)	grass shoots*	18	this study
Breeding season (adults)			
Greater Snow	grass shoots & sedge stems	14	Gauthier (1993)
Pink-footed	grass shoots*	6	Fox (1993)
Greater Snow	dicot catkins & grass shoots & roots	12	Gauthier (1993)
White-fronted	herbs & sedges	13	Madsen & Fox (1981)
Brent	mosses	5	Madsen *et al.* (1989)
Barnacle	herbs & mosses	51	Prop *et al.* (1980)
Hawaiian (Volcanoes)	berries	28	this study
Hawaiian (Haleakala)	grass shoots*	13	this study
Post-breeding season (goslings)			
White-fronted	Horsetails	14	Madsen & Fox (1981)
Cackling Canada	grass shoots	5	Sedinger & Raveling (1984)
Brent	mosses & herbs	5	Madsen *et al.* (1989)
Hawaiian (Volcanoes Haleakala)	herb shoots*	12	this study

[1] White-fronted *Anser albifrons*, Barnacle *Branta leucopsis*, Canada *Branta canadensis*, Lesser Snow *Anser caerulescens caerulescens*, Greater Snow *A. caerulescens atlanticus*, Pink-footed *Anser brachyrhynchus*, Brent *Branta bernicla*, Cackling *B. canadensis minima*.

nest and less dense vegetation in which to forage. This determines the number of nests that will fit in an area. **Figure 6** shows the first attempt to identify all potential nest locations in a selection of sites. Only ten of the 30 potential nest sites were used, which means that the area could accommodate an additional 20 nests. We suspect that the criteria Nene use when choosing nest sites is more stringent than ours, so the actual number available may be less. This means that the Volcanoes population will be soon at the upper limit of nest site availability (discussed below).

Table 14. Use of landscape types by nesting Nene pairs and associated cultivated grasslands that were used during incubation recesses. Symbols: (+) = used the area, (-) = did not use the area and (s) = suspected use of the area but not confirmed.

Landscape type	Pair #1	Pair #2#9	Pair #3	Pair #4	Pair #5	Pair #6	Pair #7	Pair #8
lava desert	+	+	+	-	-	+	+	-
cinder field	-	-	-	+[a]	+	-	-	+
Associated grassland								
HWH corral	+	+	+	-	-	-	-	-
KN Campgr.	-	-	-	-	-	+	+	-
Golf Course	-	-	-	-	s	-	-	s

a = Pair #4 flew to the Devastation Trail area to feed on herbs (Gosmore and *Buddleia sp.*).

Grasslands for geese?

Nene are opportunistic in food choice and use a wide range of food items. During the breeding season, they feed mainly on berries and other plant items found in natural vegetation on lava flows. During the pre- and non-breeding season, their principal foods are cultivated grasses. Nene are not exceptional in this respect. Other goose species use natural habitats during breeding, whereas during the non-breeding season human cultivated plants predominate in the diet (**Table 13**). Elsewhere, goose populations are rapidly increasing in number since they have shifted to feeding on agricultural land during winter (Owen & Black 1990, 1991, Cooch & Cooke 1991, Madsen 1991). Likewise, Black *et al.* (1993) argue that the main reason that the 245 Nene on Hawaii are surviving today is because they abandoned their release sites in dry volcanic montane scrub habitats in favour of the nearest grasslands. Provided that the Hawaiian grasslands are managed to produce a high quality food Nene may also benefit from using this "artificial" habitat. There is support from palaeotology that Nene originally occurred in this habitat: Olson & James (1991) found numerous Nene fossils in areas where native grasslands probably once predominated.

At Volcanoes, some of the breeding pairs supplemented their berry diet by flying to grassland at some distance from the nest (**Table 14**); at Haleakala all incubating pairs used pastures. In order to clarify when pasture feeding would occur, we calculated the food intake per recess of a standard duration of 25 minutes for geese staying in the territory to feed on berries, and for individuals flying to a pasture (**Figure 29**). The food intake at the territory depends on the density of berries (see also **Figure 26**) and the time lost walking from bush to bush. The amount ingested at the pastures depends on the time lost flying from the nest to the pasture. As long as the berry density exceeds four berries per standardized bush, the intake per recess would be highest for birds staying to feed on the lava flows (**Figure 29**). At lower berry densities, it becomes more profitable to fly to a pasture, at least when the distance to the pasture is short. Berry densities decreased gradually throughout our study period, but the decrease may be more sudden after long dry periods or after a night of frost (as occurs on higher elevations, Woog 1993). When this happens, access to a pasture will help Nene to complete incubation to hatching.

Management implications

Providing high quality pastures appears to be one of the keystones in saving the Nene from extinction. High quality pastures are essential during the non-and pre-breeding season, during the brood-rearing period (Banko 1992), whereas pastures may be an important secondary feeding habitat during the nesting phase.

In the past, a hands-off approach to Nene recovery was used once birds were released. We argue that in order to save the Nene, managers will have to employ a prolonged, intensive hands-on approach (also see Black *et al.* 1993, Black in press). The ultimate goal remains the same - self-sustaining wild populations, so that captive-bred birds will no longer be needed. In order to achieve that goal, however, habitats will probably have to be sustained well into the future and the emphasis in the agricultural industry must change to more 'goose friendly' crops, e.g. from sugar and pineapple to lush grasslands or grain.

Managers now know that traditional upland habitat can not sustain Nene throughout the year and that current mid- to low-elevation grasslands, apparently the birds' preferred feeding habitat, are not sufficient without intensive management (Black *et al.* 1993, this paper). Based on the understanding that small isolated populations will eventually become extinct (e.g. in general, 400 to 500 animals are needed to maintain 90% of starting heterozygosity), management must be on a grand scale.

Black *et al.* (1993) suggested that a series of predator-proof areas enclosing well-managed refuges could be set up throughout the State, reviving Sir Peter Scott's (1962) 'Nene Parks' concept. We suggest that several large refuges (private or State/Federal), on a par with waterfowl refuges on mainland North America and Europe, need to be created albeit in terms of hundreds of hectares rather than thousands. We can easily imagine that refuges could be managed for a minimum of 2000 geese on Maui, 2000 on Kauai and 5000 on Hawaii, totalling 9000. Nene may also be supported on other islands. To enable gene flow between refuges and islands, the birds should be encouraged to fly or taught flight paths between sites. In order to achieve success at this level the support of the Hawaiian people at all levels will be needed. Therefore, a 'Community Education Plan for Nene-Awareness to Action' must be supported as an integral part of the recovery programme (Black 1991, Dietz *et al.* 1994).

The refuges should consist of large areas of vegetation that are farmed specifically for Nene, expanses of appropriate nesting habitat (natural and/or artificial, see below) and water sources. The options that are available to managers for enhancing existing grasslands include grazing, mowing, burning, fertilizing and irrigation -all of which are known to improve the foraging conditions, subsequent survival and reproductive success of a variety of birds (Miller *et al.* 1970, Ball *et al.* 1981, Owen & Black 1990). Farming for endemic legumes could also be initiated. The refuges should be maintained as predator-free areas through initial massive eradication and continual control programmes. Refuges should be located near to natural scrubland nesting habitat, as at Volcanoes and Haleakala, as Nene in these areas will continue to utilise the full range of foraging skills that characterise the species.

If Nene were established in some of the 0.5 million ha of private land that is managed for cattle grazing, appropriate nest sites may not be readily available for the geese. In such situations, Nene might learn to use artificial nest platforms -a conservation technique that has been hugely successful with Canada Geese *Branta canadensis* (eg Brakhage 1965). The platforms would have to screen mongooses effectively and give protection from the sun; platforms could be built within large bushes or trees or large, open-fronted nest boxes could be used. A period of research in captivity may indicate which platform type would be most successful. Nene in Hawaii are also known to nest under man-made structures (e.g. Kahuku Ranch and Puu Waawaa Ranch). The Nene at Slimbridge nest readily under wind-proof 'wigwam' structures made of willow branches (Kear & Berger 1980).

Several improvements could be made to the areas we studied. In order to produce high quality forage, all existing grassland areas could be harvested (by mowing or intensive livestock grazing) at frequent intervals. The regrowth of plant tissue could be enhanced, not only with fertilizers, but with an irrigation regime in those areas without sufficiently high rainfall. Rotational harvesting, in large swaths, might facilitate a gradient of growth, from new shoots to seedheads. Frequent harvesting would ensure a continual supply of young shoots. We envisage such management at Paliku Pasture, Ainahou Ranch, Halfway House pasture, Kapapala Ranch and Kipuka Nene Campground. Due to the high rainfall at Haleakala, a regular routine of mowing at the Paliku pasture would perhaps yield the greatest quantity of quality forage.

The question of foraging skill in the Nene

Researchers and managers suspected that captive-reared Nene may not possess adequate foraging skills after release into the wild (Stone *et al.* 1983a). Banko (1992) proposed that inadequate foraging skill, which limited food intake, was one reason why few pairs attempted to nest each year. There is some evidence that captive-reared Nene have poorly developed social skills (Marshall & Black 1992), but captive diets do not appear to influence negatively food choice after release (Rojek pers comm). Our study indicates that some Nene do indeed possess highly developed foraging behaviours. We have shown how Nene are capable of utilising the sparse Kau Desert vegetation, which is certainly on a par with the adept behaviour of arctic geese foraging on tundra vegetation. The fact that three of the birds in our study, which were released as goslings less than 20 months earlier (**Table 1**), succeeded in hatching goslings suggests that Nene can learn quickly the required level of foraging skills. These birds were reared by their parents and released with foster parents.

The other reason that managers suspected a link between low Nene productivity and food supply was because the birds' staple foods had been out-competed by the many invading exotic plants (Stone *et al.* 1983). We provided some evidence that the Nene's diet has, indeed, changed in favour of the the invader species. Between 1938-1944, Baldwin (1947) identified 31 different plant species from 543 droppings from the Kau Desert, Puu Waawaa, Mauna Loa (Volcanoes National Park), Humuula and Hualalai (all on Hawaii Island). The most abundant item found in the droppings was the endemic hairgrass. In the present study, this species was identified only in droppings from Haleakala. In the droppings of Nene using the Kau Desert, Baldwin found only eight species of plant, whereas we found a total of 26. It seems there has been a change in either the birds' behaviour or the vegetation over the last 50 years. The latter is more likely since endemic and indigenous plant species are out-competed by more vigorous, introduced species resulting in a decline in availability of the former vegetation (Cuddihy & Stone 1990). However, we suspect that the change in diet may have actually enabled the Nene to survive and reproduce in new areas, like the Kau Desert (also see Black in press). Nene seems to do well on these 'new' foods (**Figure 28**).

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Appendix 1 - Survey of the predominant vegetation in nesting territories. Values are number of plants per m^2 except for sand and vegetation cover which are mean percent of ground area (Nests 1 - 7 are at Volcanoes, 13 is at Haleakala).

Species	Nest 1 *n*=54	Nest 3 *n*=46	Nest 4 *n*=56	Nest 5 *n*=30	Nest 6 *n*=46	Nest 7 *n*=57	Nest 13 *n*=14
Pukiawe	0.164	0.143	0.156	0.393	0.203	0.163	2.300
Ohelo	0	0	0.081	0.004	0	0	67.600
Ohia	0.021	0.012	0.012	0.001	0.003	0.008	0
Aalii	0.318	0	0.125	0.279	0	0.206	0
Beardgrass	0.975	0.348	0	0	0.522	0.210	0
Broom Sedge	0.156	0	0.144	1.671	0	0	0
Molasses grass	0.136	0.111	0.002	0.179	3.200	0.924	0
Sedge *B.capillaris*	2.252	0	0.001	0.033	0	0	0
Gosmore	0	0	0	0	0	0	51.600
Yorkshire Fog	0	0	0	0	0	0	19.500
Hair Grass	0	0	0	0	0	0	5.400
Kukaenene	0	0	0	0	0	0	1.700
% sand/cinder	23.43	21.85	100	75.86	45.13	14.74	-
% veg. cover	14.94	-	8.84	31.69	-	-	-