Distribution and timing of nesting in Hawaiian Geese in relation to food phenology in scrublands

F. Woog

The Wildfowl & Wetlands Trust, Slimbridge, Gloucester GL2 7BT, UK.
Present address: Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1,
70191 Stuttgart, Germany. Email: woog.smns@naturkundemuseum-bw.de

The seasonal distribution patterns of individually marked Hawaiian Geese or Nene *Branta sandvicensis* are described in relation to the availability of their food plants in scrubland. The phenology of the most important plant groups was recorded over a 18 month period, and goose numbers and nesting activity monitored. Plant phenology varied considerably between species, between sites and with elevation. Geese appeared to time their movements and nesting according to local food availability. The analyses of a long-term database on nest records (1960 -1996), revealed that peak nest initiation was in November and December, coincident with high average rainfall. Generally, geese that nested earlier in the season, when berry availability was high, were more successful in rearing young, but other events such as predation, caused some early breeders to fail.

Key Words: Food availability, breeding, annual cycle, endangered *Branta sandvicensis*

Food availability is a key factor governing animal distribution (Krebs 1978; Newton 1980). Herbivores assess the quality of their food, and 'track' resources by switching sites, diet or both when they are depleted (Drent & Prins 1987; Sedinger & Raveling 1984). The reproductive success of arctic geese is influenced by the availability of food in the winter and spring staging grounds (Ankney 1977; Ankney & McInnes 1978; Raveling 1978; Ebbinge 1989; Prop & Deerenberg 1991). Arctic Geese are thought to time their nesting so that food plants in their nesting habitat are abundant and provide maximum nutrition when goslings hatch (eg Ely & Raveling 1984; Sedinger & Raveling 1986). Although Hawaiian Geese have an arctic origin (Quinn *et al.* 1991), they have evolved as a non-migratory species that lives in subtropical habitats. In the tropics and subtropics, many fruit and nectar-feeding birds migrate locally according to food availability (Sick 1968; Wolf 1970; Leck 1972).

There are few historical accounts of foraging and seasonal habitat use by Hawaiian Geese. Some authors have suggested that before their near extinction in the mid-twentieth century, Hawaiian Geese bred and moulted in the lowlands (below 400-700m). In these areas, they are thought to have fed on fresh plant growth in the wet winter months, but migrated to higher altitudes when food resources became scarce during the drier summer months (Henshaw 1902; Perkins 1903; Munro 1944; Baldwin 1945, 1947). Today, there is no evidence of such an elevational migration, although birds do move between locations throughout the year.

Since 1974, over 260 Hawaiian Geese have been released as a conservation measure in Hawaii Volcanoes National Park and adjacent ranch land. The birds have subsequently dispersed from the release sites into different scrubland and grassland areas. In grasslands, the diet varies spatially and temporally, and birds feed preferentially on plants of high nutritional quality (Woog & Black 2001). Prior to nesting, most breeders accumulate fat reserves in grasslands (Black *et al.* 1994). During nesting, birds forage within their breeding habitat primarily for berries on shrubs that grow on lava flows with little vegetation cover, but birds will also fly to grasslands to feed (Black *et al.* 1994). After hatching, parents typically lead their young to adjacent grasslands, that consist primarily of non-native plant species managed through grazing or regular cutting. During the non-breeding season, Hawaiian Geese disperse away from the breeding areas (Banko & Elder 1990), and aggregate in flocking areas. Moulting areas are dispersed throughout remote desert areas where there is little or no vegetation.

There is large geographical, annual and seasonal variation in rainfall in Hawaii that causes fluctuations in food availability for the geese (Banko 1988; Black *et al.* 1994). In summer, the prevailing northeastern trade winds bring a gradual supply of rain to the windward areas, whereas leeward areas remain drier. The winter months are usually wetter as a result of storms bringing rain from the south, although droughts in the leeward areas are common when the winter storms fail to occur (Armstrong, 1983). The climate of high altitude sites is affected by an inversion layer that forms above 1,200 - 2,400m, and is present for about seventy percent of the time causing areas above it to be arid (Giambelluca *et al.* 1986).

Poor availability of food is thought to be a major limitation in the productivity of Hawaiian Geese (Baldwin 1947; Stone *et al.* 1983; Banko 1992; Hoshide *et al.* 1990). Understanding how Hawaiian Geese respond to the fluctuations in the abundance of their food plants, and how this may be a function of fluctuations in rainfall, is crucial for conservation management during the breeding and non-breeding seasons.

This paper is in three sections. The first explores habitat use of the Hawaiian Goose population within Hawaii Volcanoes National Park by comparing monthly re-sighting frequencies of marked birds in scrublands with other habitats. The second explains variations in goose distribution, seasonal berry availability and young plant growth in scrublands in relation to rainfall. The third examines the timing of nesting in relation to food availability and rainfall.

Study areas

Hawaii Volcanoes National Park (19°15'N, 155°15'W) comprises an area of 85,000 ha ranging from sea level to 4,164m on the summit of Mauna Loa. Geese mainly utilize the mid elevation desert scrublands and small grassland patches (600 - 1,200m). A few birds have been seen at sea level whilst others occur as high as 2,100m in the remote vegetation patches surrounded by lava (Kipukas) of the subalpine zone. Habitats were classified into three types: open scrubland, grassy scrub and grasslands. Scrublands were open, volcanic desert with scattered bushes. Grasslands were managed pastures with predominantly grass cover. Grassy scrub was a mixture of shrubs and unmanaged tall grasses.

Eight volcanic, open scrubland areas along an elevational gradient were studied between October 1994 and March 1996, encompassing two breeding seasons and one summer flocking season (**Figure 1**). Hawaiian Geese have previously nested in all study areas.

'Three Trees Kipuka' (Site 1) is a high altitude ecotone, located on Mauna Loa at the interface of the montane and subalpine zones. It is a vegetation island on a smooth lava surface surrounded by rough, unvegetated lava flows. The main foods available are Pukiawe *Styphelia tameiameiae*, Kukaenene *Coprosma ernodeoides* berries and Gosmore *Hypochoeris radicata*, some *Rumex acetosella*, as well as several native and introduced grass species (*Deschampsia nubigena, Anthoxanthum odoratum, Eragrostis sp., Holcus lanatus*).

'Devastation' (Site 2) and 'Crater Rim' (Site 3) were located in the montane seasonal zone with a dry summer climate, and both have volcanic cinder substrate. Vegetation cover at Site 3 is sparse, but includes Pukiawe, Ohelo *Vaccinium reticulatum* and some introduced grasses along roadsides. The site is often exposed to wind and volcanic fumes from the nearby Kilauea Crater. In contrast, Site 2 is sheltered by surrounding forest, receives more

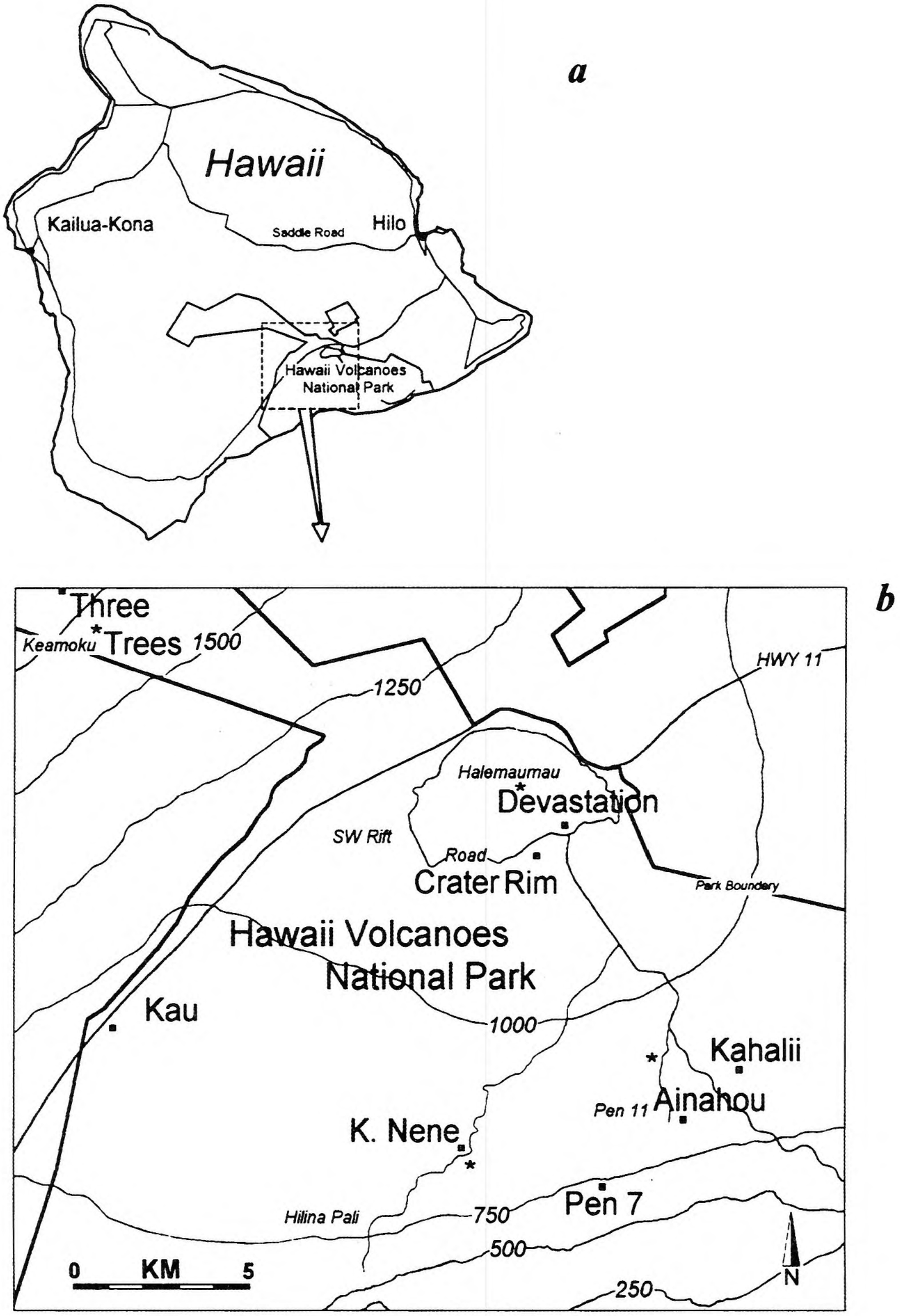

Figure 1. The island of Hawaii with Hawaii Volcanoes National Park and scrubland study sites (indicated with a square) within the National Park. *= weather stations run by the National Park; contours at 250m intervals.

rainfall, and vegetation cover is greater in most parts. Introduced plant species such as *Buddleia asiatica*, *Andropogon virginicus*, Pamakani *Ageratina riparia*, Blackberry *Rubus argutus* and Gosmore grow alongside natives such as *Rumex skottsbergii, Dubautia scabra* and Ohelo. Most geese nesting around the southern part of Site 3, including Keanakakoi Crater, lead their goslings to Site 2 to forage.

The remaining study sites are situated on the southern slope of Kilauea and have a dry summer climate. The desert around 'Kipuka Nene' (Site 4) is open, mesic scrubland on a smooth lava flow, dominated by Pukiawe, Aalii *Dononaea viscosa* and Ohia *Metrosideros polymorpha*, with scattered grasses, mainly introduced *Andropogon, Melinis minutiflora* and the native sedge *Bulbostylis capillaris*. The lava flow east of the former Ainahou ranch (Site 5) is dominated by Ohia, Pukiawe, Aalii and scattered Uulei *Osteomeles anthyllidifolia* and, compared to the other study sites, has the highest density of introduced grasses such as *Andropogon* and *Melinis*. 'Kipuka Kahalii' (Site 6) is a cinder field surrounded by open, mostly unvegetated smooth lava flows. Mamaki *Pipturus albidus* bushes predominate at this site and grow over two metres tall, but geese exploit large parts of the bushes by climbing into them. Other species used by the geese include introduced *Buddleia*, and native *Rumex* and *Dubautia scabra.* The southwestern part of the 'Kau' desert (Site 7) is dominated by Pukiawe and Ohia shrubs with some Aalii, introduced grasses such as *Andropogon* and *Melinis* and the native sedge *Bulbostylis*. 'Pen 7' (Site 8) is a comparatively dry lowland site, in the vicinity of an open-top breeding pen. The main attraction for the geese is probably the supplemental food inside the breeding pen, but natural vegetation is eaten as well. Aalii and Pukiawe are predominant with scattered introduced grasses.

Methods

Study population

Since the first releases into the wild in 1974, Hawaiian Geese in the Hawaii Volcanoes National Park have been individually marked with leg rings. In addition, most progeny of released birds have been ringed prior to fledging, resulting in over 90% of the population being marked. The rings are made of either aluminium, coloured plastic or recently, Darvic engraved with a unique letter code, and can be read through a telescope or binoculars. By 1996, the population had grown to approximately 160 individuals.

Counts and resighting data

Between October 1994 and March 1996, most areas utilised by Hawaiian Geese were searched and counted at least weekly. During goose counts, ring number, location, date, time of day, mate and number of associated goslings were recorded. Data were collected between 0800 and 1600h. The largest flock count recorded in a given month (monthly maximum number of geese) at Site 6, an important flocking area since 1981, was used as an index of habitat use for that site. It was not meaningful to compare maximum goose counts between the other sites because birds were dispersed during nesting and observed goose numbers were low. Therefore only the combined monthly number of individuals seen at three scrubland sites were used (Sites 3, 4 and 5). Re-sightings data of marked individuals were used to compare differences in habitat use between months.

Nest searches

Between October and March (the breeding season), all study sites were surveyed regularly for nesting activity. Searches in the desert nesting habitat were conducted using parallel transects 20-30 metres apart, depending on vegetation densities. Clutch size was noted for each nest, and nesting success classified as young successfully hatched/fledged, or no young hatched/fledged (failed). The lay date was either noted directly in the field, or estimated from the hatch date or, alternatively, estimated from the date when a pair was seen with up to one-week-old goslings (the G1 stage as described by Hunter 1995). Known second clutches were excluded from the analysis. In addition to the data collected for this study, long-term nesting data from 1975/1976 onward were available, allowing an analysis of the timing of nesting and seasonal trend in clutch size. Nest initiation dates of individual birds were compared by counting the days between lay dates in consecutive years.

Plant phenology transects

At each site, three parallel transects, 200m long and 100m apart, were established using measured lengths of twine and following randomly selected compass bearings. Transects were subdivided into ten 20m sections. Key food plant species were selected according to their known importance in the Hawaiian Goose diet, based on faecal analysis (Black *et al*. 1994) and from personal observations (P. Banko, H. Hoshide, D. Hu.). Within each 20m section, one of each key food plant species was marked and numbered. This resulted in 30 individual plants of each species being marked at each site (**Table 1**). Bushes were selected at random to provide a distribution of sizes available at each sample site. Species included Pukiawe, Ohelo, Uulei, Mamaki, *Rumex skottsbergii, Dubautia scabra, Buddleia asiatica* and Pamakani.

Kukaenene and Florida Blackberry grew in clumps and in small numbers, and a different survey method was therefore used. Thirty individual branches were marked with numbered poultry rings, and distributed over three to four bushes.

Phenological measurements included intensity of vegetative growth or flush (*Rumex, Dubautia, Buddleia* and

Table 1. Study sites and the native or introduced Nene food plant species marked. The main food source is indicated.

Site		Native species		Introduced species
		Berries	Leaves	Leaves
1	Three Trees Kipuka	Pukiawe, Kukaenene		
2	Devastation	Ohelo, Kukaenene	*Dubautia*, *Rumex*	*Buddleia*, Pamakani
3.	Crater rim	Pukiawe, Ohelo		
4	Kipuka Nene	Pukiawe		
5	Ainahou	Pukiawe, Uulei		
6	Kipuka Kahalii	Mamaki	*Dubautia*, *Rumex*	*Buddleia*
7	Kau Desert	Pukiawe, Uulei		
8	Pen 7	Pukiawe		

Pamakani) and an estimation of the number of ripe berries (Pukiawe, Ohelo, Uulei and Mamaki). Vegetative flush was assessed in the following categories (adapted from Bridges *et al.* 1981): A = no occurrence, B = little or occurrence on less than a third of the branches, C = moderate or occurrence on more than a third of the branches and D = heavy or occurrence on more than two thirds of the branches. The number of ripe berries was estimated to the nearest 10 on bushes, and counted individually on marked branches. All plants were monitored on a monthly basis. Plant density in each scrubland study site was assessed in randomly chosen 10 x 10m quadrates.

Meteorological data

Rain gauges and minimum-maximum thermometers were placed in each study area, and data collected on a weekly basis. Before the study, from 1988 onwards, rainfall records were available for some of the sites. To test whether rainfall patterns affected the timing of nesting, rainfall from the weather stations were assigned to the nearest study areas as follows: data from 'Keamoku' (1,700m) were assigned to Site 1, data from 'Halemaumau' (1,100m) to Sites 2, 3 and 7, data from 'Kipuka Nene' (850m) to Site 4 and data from 'Ainahou' (914 m) to Sites 5 and 6. Rainfall before nesting may affect the food resources that a female can accumulate prior to laying, and therefore affect clutch size. Rainfall during incubation may affect incubation performance, and rainfall after hatching may affect plant growth which is important for gosling growth and survival. Monthly sums of rainfall (mm) were therefore taken before, during, and after the month of nest initiation and classified as either dry

(<100mm monthly rainfall) or as wet (≥100mm). The number of nests initiated in each month was then compared with monthly rainfall.

Data analysis

To evaluate differences in habitat use, the proportion of ringed birds seen each month in open volcanic scrubland was compared with the proportion of birds that were re-sighted in other habitat types (grassy scrub and grasslands) using a binomial error distribution in GLIM (Crawley 1993). To avoid pseudo replication, paired geese and single birds were treated as one unit. If birds were seen more than once per day, one re-sighting was randomly selected. Re-sightings in and around breeding pens with access to food were excluded from the analysis. Data were over-dispersed and, because the denominators were unequal, this was controlled for by using William's procedure (Crawley 1993). After adjusting for over-dispersion, *F*-values were used instead of χ^2-values. Month was added as a factor and rainfall added as a continuous explanatory variable. For plotting purposes, proportion data were arcsine transformed.

To determine the monthly relative abundance of ripe berries, an index was calculated by summing the monthly berry counts on 30 bushes for each site and species separately (using the method described by Bridges *et al.* 1981). Indices for Blackberry and Kukaenene berries were derived by summing berries counted on the 30 individually marked branches. Because Mamaki bushes were large and berries difficult to estimate, phenology of ripe Mamaki berries was assessed by counting the maximum number of berries found on a branch for each bush, and then summing the maximum counts for 30 bushes. To get an index of vegetative growth, the indices for the 30 plants in each study site were summed. The phenological measurements provided an index of food availability at the time of measurement. Data dependency between monthly measurements prevented an analysis of correlation between rainfall, berry availability and maximum flock sizes. The phenology results are therefore mainly descriptive. A seasonal trend in clutch size was investigated in an analysis of variance in GlIM (Crawley 1993) with a normal error distribution using the months of nest initiation (October to February) as an explanatory variable .

Results

Meteorological data

Minimum temperatures, which potentially limit plant growth (Begon *et al.* 1996), were lowest at the high elevation site (Site 1) and highest at the low elevation site (Site 8; **Figure 2**). In 1995, January and February were the coldest months, August through October were the warmest (**Figure 2**). Annual rainfall was highest at Sites 2 and 6, intermediate around Sites 3, 4 and 5 and lowest at the high elevation site (Site 1), low altitude site (Site 8) and Site 7 (**Figure 3**).

Between 1988 and 1995, the highest average rainfall was recorded between November and January and the lowest in June (**Appendix 1**). Monthly rainfall varied considerably between sites (**Appendix 2**) and years (**Appendix 3**). Between 1988 and 1995, monthly rainfall at Site 1 was the most variable (ie in February: 2 - 430mm), followed by Site 4 (in March: 5 - 440mm). Over the study years, February was the most variable month (**Appendix 1**).

Plant density

The dominant berry bush species varied between sites (**Appendix 4**). Kukaenene was most abundant at site 1; Uulei and Pukiawe at Site 5; Mamaki at Site 6; and Ohelo, *Buddleia, Ageratina* and *Dubautia* at Site 2.

Frequency of geese re-sighted in scrublands

The proportion of individual birds re-sighted in scrublands varied between months (**Figure 4**). It was high at the onset of the breeding season in October 1994, during moult in March 1995 and in September 1995 during summer flocking. Variation in monthly rainfall during the breeding seasons

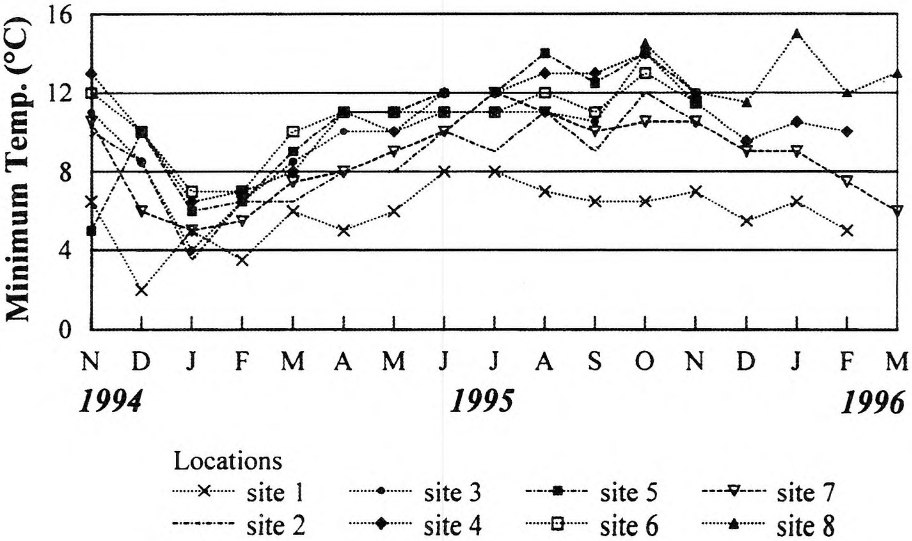

Figure 2. Monthly minimum temperatures in eight scrubland sites within Hawaii Volcanoes National Park between November 1994 and March 1996.

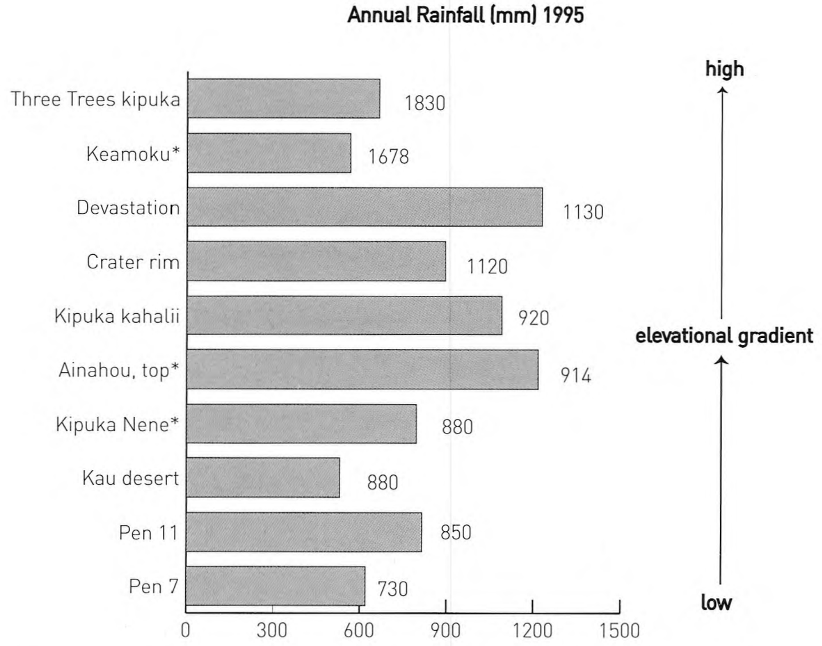

Figure 3. Annual rainfall in 1995 at sites within Hawaii Volcanoes National Park. The data marked with an asterisk are courtesy of the Hawaii Volcanoes National Park Fire Department. Numbers to the right of the bars indicate the approximate elevation of the sites in metres.

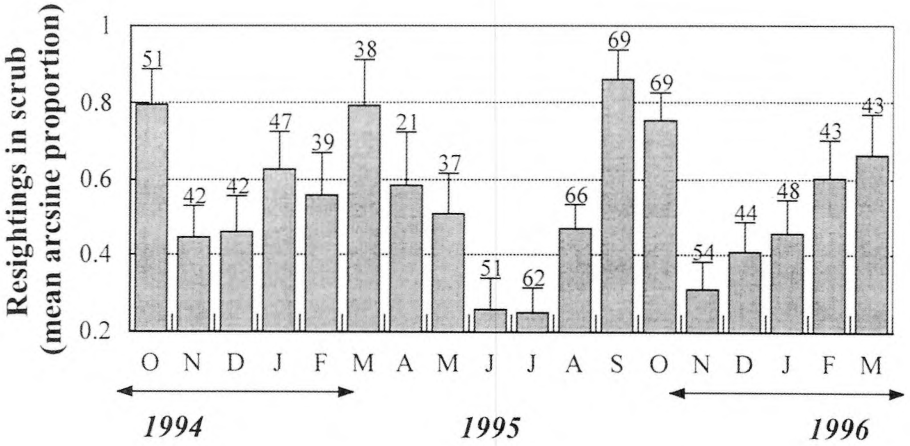

Figure 4. The proportion (mean arcsine) of individual Nene resighted in open scrubland habitat. Sample sizes (including pairs, single males and single females) and standard errors are indicated. The breeding season is indicated with an arrow.

explained a small part of the variation in re-sighting frequency in scrublands ($F=4.41$, df=1, $P<0.05$) when fitted as the single explanatory variable. However, rainfall had no significant effect when month was included (months October to March: $F=5.29$, df=5, $P<0.0001$; controlling for year: $F=4.09$, df=1, $P<0.05$). This suggests that the rainfall variation between months explained only part of the variation in goose distribution. The overall percentage of individuals re-sighted in open scrublands was similar between the two breeding seasons with 38% (1994/1995) and 37% (1995/1996). Re-sighting data for other habitats are not shown but the majority were from grassland habitat.

Phenological patterns and rainfall

Most Mamaki, Pukiawe and Ohelo bushes fruited almost continuously, but numbers of fruits fluctuated throughout the year. Blackberry and Kukaenene fruited seasonally. The production of ripe berries was synchronized within Mamaki, Blackberry and Kukaenene, but varied among individual Ohelo and Pukiawe bushes. Plants produced new leaves almost continuously and there was no coordinated loss of leaves among bushes. At most sites, Pukiawe fruited most heavily in the wet winter months when demand for berries by nesting geese was high (**Figure 5**). Fruiting by Uulei was greatest at Site 5 in September and at Site 7 in October, at the end of the dry summer (**Figure 5**). The number of Uulei berries was lower at Site 7 and fruiting peaked later, which coincided with lower precipitation in this area. Around Site 3, fruiting in Ohelo peaked three times (**Figure 6**): March, August and November-December. At Site 2, the peak in March coincided with the one at Site 3, but there were no other distinct peaks. Rainfall did not appear to affect the Ohelo fruiting pattern at these two sites.

At Site 2, the number of ripe Kukaenene berries decreased steadily between September 1995 and February 1996 (**Figure 6**). In the same time period, during the wetter winter months, Kukaenene berries at the high elevation site, Site 1, increased in numbers (**Figure 5**). At Site 6, Mamaki fruiting peaked at the end of the summer (**Figure 7**). Rainfall and the number of Mamaki berries correlated well in some months (eg between December 1994 and March 1995), but seemed unrelated in other months.

Vegetative growth activity was lowest in March and April (**Figure 8**) perhaps due to a longer-term effect of a drop in rainfall following wet winter conditions. It is unclear how the monthly rainfall data related to growth at other times.

Goose distribution in relation to berry phenology

At Site 6, geese were apparently attracted by ripe Mamaki berries from 1981 onwards, when the first geese were seen in this area (**Figure 7**). Goose numbers counted at Site 6 gradually

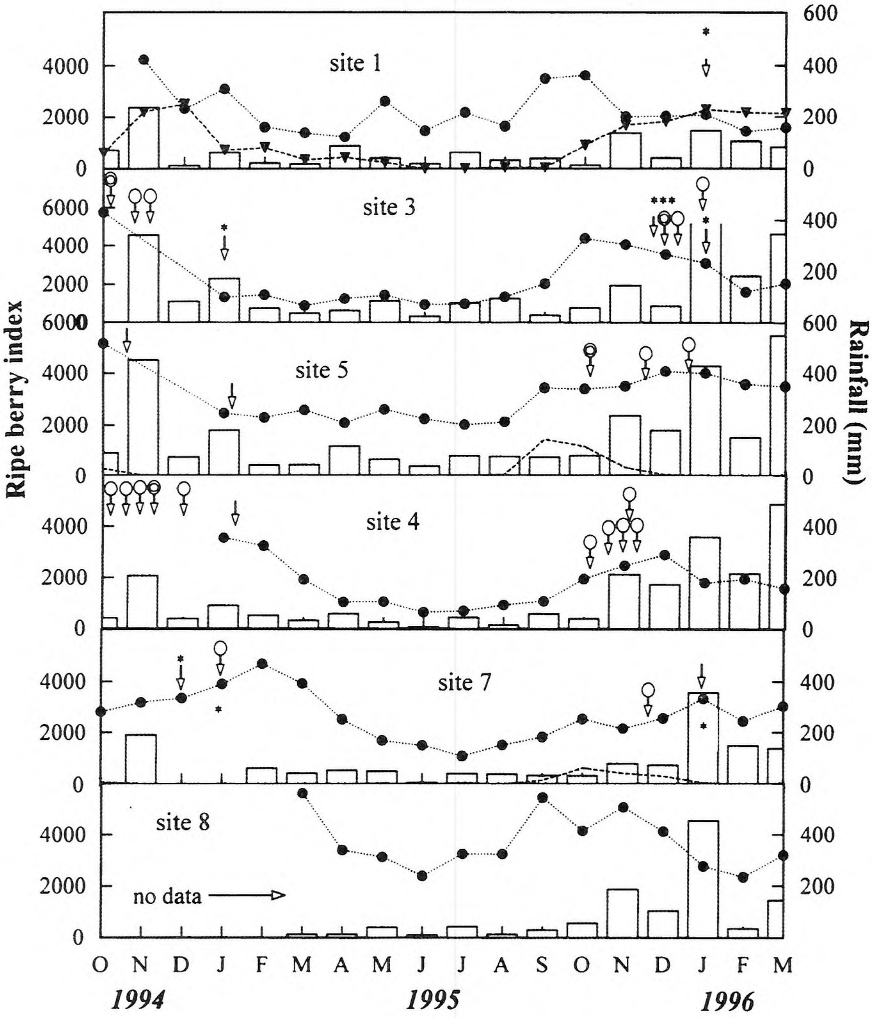

Figure 5. Phenology of ripe Pukiawe berries (filled circles), ripe Uulei berries (open circles) and Kukaenene (closed triangles, for graphical purposes multiplied by 10) at six sites between October 1994 and March 1996 in relation to monthly rainfall (indicated by histogram bars). Arrows indicate Nene nest initiation (single arrow = unsuccessful, arrow with circle = hatched, arrow with double circle = fledged). *indicates the estimation of nest initiation month from indirect evidence such as female brood patch or nest inspection after hatching.

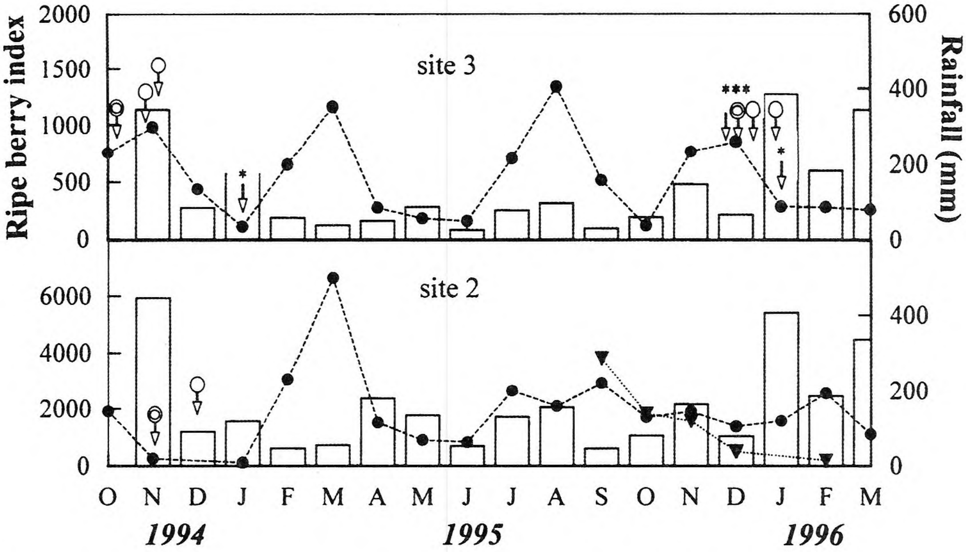

Figure 6. Phenology of ripe Ohelo berries (filled circles) at Sites 2 and 3 and Kukaenene (filled triangles) at Site 2 in relation to monthly rainfall (bars). Arrows indicate Nene nest initiation (for an explanation of the symbols see **Figure 5**).

increased to a maximum in 1995. In 1995, goose numbers were high in September coinciding with a peak of ripe Mamaki berries. At Site 2, a peak of ripe Blackberries was expected in July towards the end of the dry season based on the number of unripe berries recorded in May and June, but the berries were depleted by an unknown source, and data are therefore not presented. Blackberries apparently attracted Hawaiian Geese to Site 2 in July in some years prior to the study (Hoshide pers. comm.).

Timing of nesting

Between 1975 and 1996, Hawaiian Geese initiated nests from October to March with a peak in November and December (**Figure 9**). In those two months, 74% of all nests in the wild were initiated. Unlike in other geese (Cooke *et al.* 1995), there was no seasonal pattern in clutch size (months October to February: *F*=0.29, df=4, n.s.). Hatching and fledging success gradually declined throughout the breeding season (**Table 2**), although these trends were not statistically significant (hatching success: G=1.49, df=4, n.s.; fledging success: G=6.13, df=4, n.s.). Timing of nesting in consecutive years varied considerably for some individuals. The mean number of days between nest initiation dates in different years was 16.6±2.1 days (n=50 nest initiation date comparisons of 17 females). Some females varied nest initiation dates in

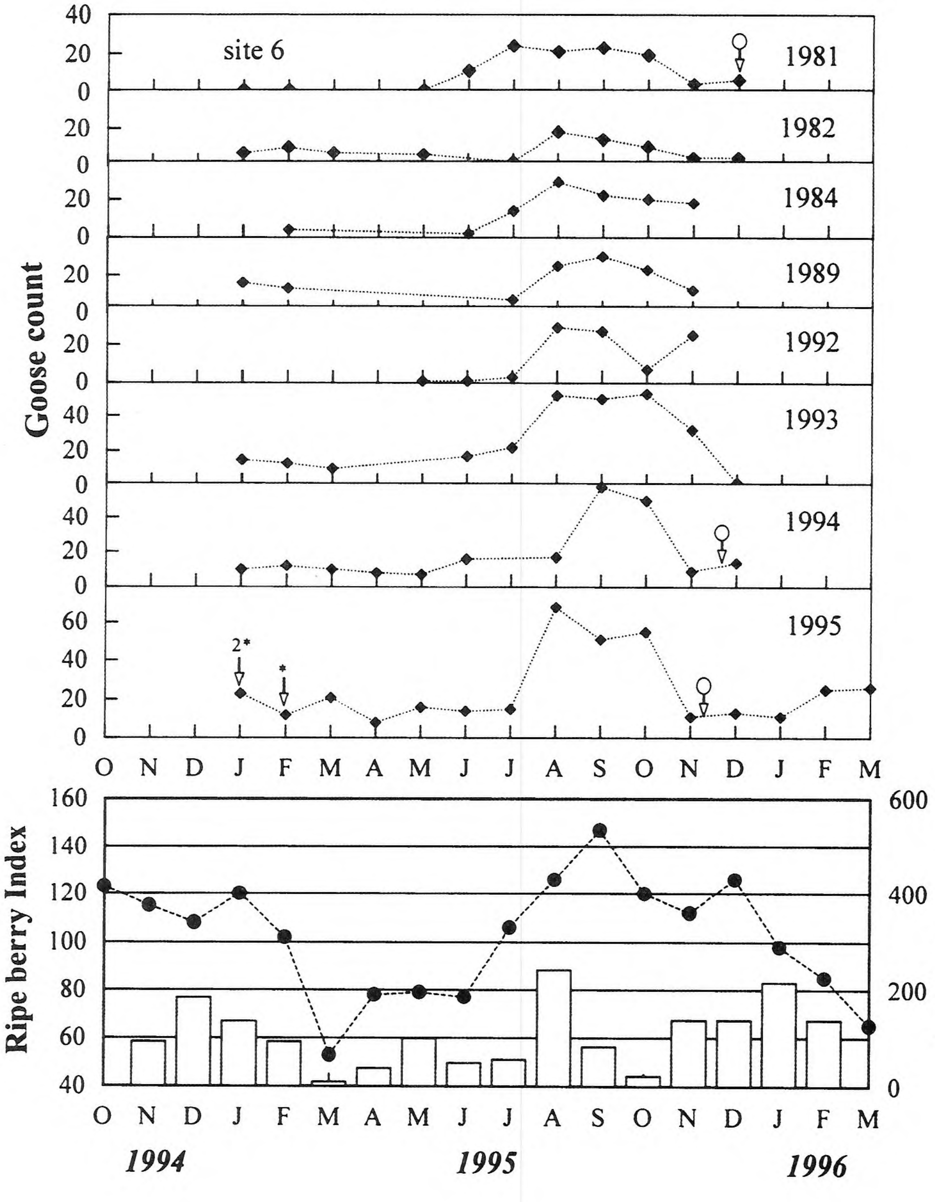

Figure 7. Monthly maximum number of Nene sighted at Site 6 in selected years between 1981 and 1996 (upper graphs) in relation to the phenology of ripe Mamaki berries (dots, lower graph) and rainfall (bars, lower graph). Years that are not presented had either a poor resighting effort or were similar to the above pattern. Arrows indicate Nene nest initiation (for an explanation of the symbols see **Figure 5**).

some years, but not in others (eg they laid exactly on the same day in their first and second year, but in the third year they nested 10 days later).

Timing of nesting in relation to rainfall and plant phenology

Most nests were initiated between November and January, which had high average rainfall (**Figure 10; Appendix 2**). Not all November and December months, however, were wet (**Appendices 1 and 3**). Analysing the long-term nesting data on a monthly basis revealed that patterns of nest initiation were not related to actual monthly rainfall before, during or after incubation (**Figure 10**). During the study, most nesting occurred at Sites 3, 4, 5 and 7 (**Table 3**). In 1996, nests in three study sites (Sites 3, 4 and 5) were initiated when the number of ripe Pukiawe berries was at a peak (**Figure 11**). The monthly number of individual birds re-sighted at these sites peaked in November and December, one month after the summed indices for ripe Pukiawe berries (**Figure 11**). Although the number of nest records during the phenology study were small, early broods tended to be more successful, reflecting the trend in the long-term data. In 1994, only the earliest brood fledged at Site 3. The goslings hatched when Pukiawe and Ohelo (**Figures 5 and 6**) availability was high. In addition, the family used site 2 and might have depleted Ohelo berries there. In January, when most of the berries were depleted, the young birds were able to take advantage of increased young growth in plants (**Figure 8**); young goslings were observed to forage on young *Buddleia* leaves and some *Rumex* plants showed signs of heavy browsing. Lush growth in Gosmore, an important gosling food, (Black *et al.* 1994), was high in January. In 1995, only the earliest brood at Site 5

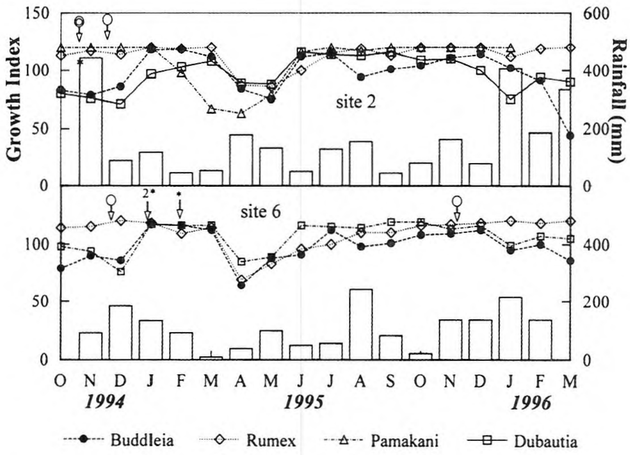

Figure 8. Vegetative growth in four plant species at Sites 2 and 6 in relation to monthly rainfall (bars). Arrows indicate Nene nest initiation (for an explanation of the symbols see **Figure 5**).

Table 2. Hatching and fledging success of Nene in relation to month of nest initiation at Hawaii Volcanoes National Park (1975-1996).

	Hatching			Fledging		
	Success	Fail	% Success	Success	Fail	% Success
October	11	1	92	5	7	42
November	30	3	91	9	21	30
December	20	3	87	3	15	17
January	3	1	75	0	4	0
February	3	1	75	0	2	0

Table 3. Number of Nene nests (or females showing evidence of breeding) found during the 1994/1995 and 1995/1996 breeding seasons. Only nests for which hatching date was known or could be estimated are presented.

	Number of nests	
Site	1994/1995	1995/1996
2	2	0
3	4	6
4*	12	8
5**	4	6
6	4	1
7	4	6
Unknown***	6	3
Total	36	30

* includes Hilina Pali
** includes Lower Ainahou
*** includes indirect evidence of nesting (eg brood patch)

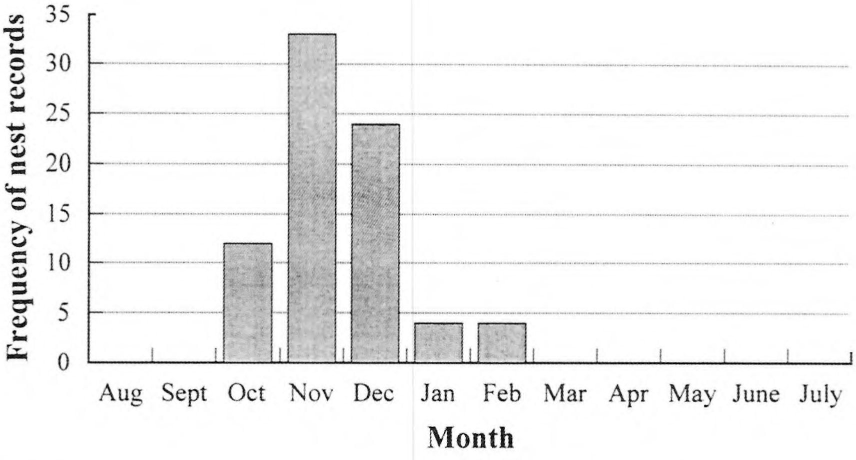

Figure 9. The frequency of Nene nest initiation between 1975 and 1996 (as determined by lay date) in Hawaii Volcanoes National Park in the wild (n=77). Second clutches were excluded.

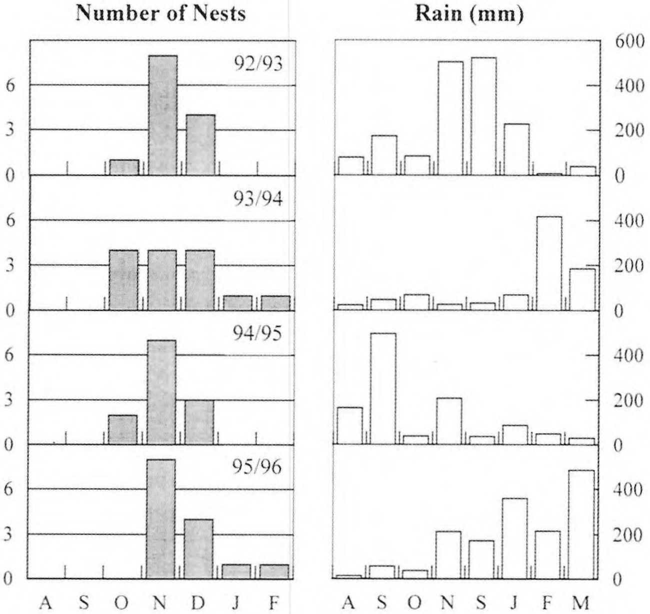

Figure 10. Number of Nene nests initiated between the 1992/1993 and the 1995/1996 breeding seasons and monthly rainfall from a central point in Hawaiian Goose habitat (Kipuka Nene).

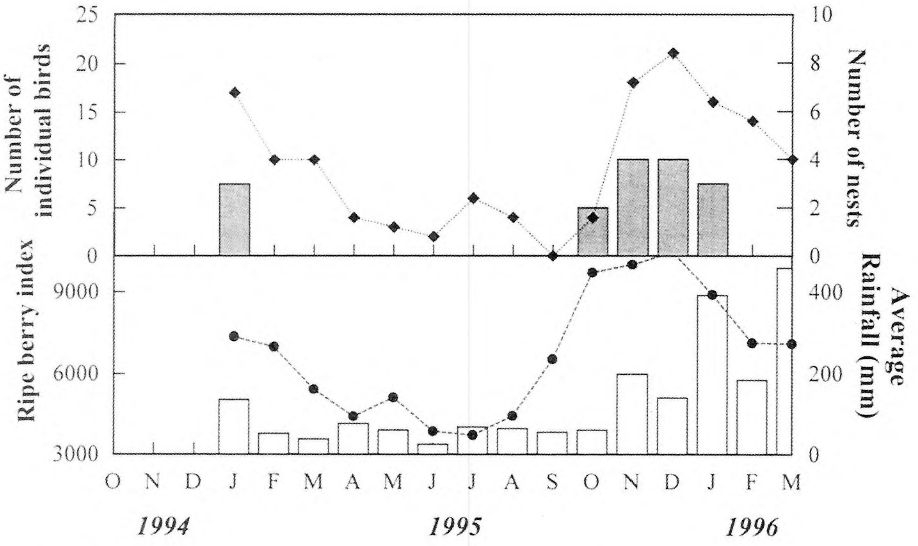

Figure 11. The monthly number of individual Nene resighted at Sites 3, 4 and 5 (dotted line with diamonds) in relation to the number of nests initiated there (grey bars), the phenology of ripe Pukiawe berries (lower line with dots; indices of all three areas combined) and average rainfall (bars, lower graph).

fledged. The first nest was active during a period of high berry availability with both Uulei and Pukiawe abundant, whereas later only Pukiawe berries were abundant, but Uulei berries were not available. At Site 6, only early nests, initiated during periods of relatively high Mamaki berry availability, hatched young successfully (**Figure 7**). Nests initiated later, in January and February, preceded the lowest availability of Mamaki berries in March and failed without exception. Some early nests failed due to external events such as predation and severe weather. In 1994, a nest initiated at Site 5 in October was predated by a dog. In 1995, a gosling hatched from a nest initiated at Site 4 in October disappeared after a storm.

Discussion

The main findings in this study are that plant phenology varied substantially and often unpredictably between years and sites. The geese actively tracked and exploited patchily distributed food resources, and moved to areas with high berry abundance and appeared to time their nesting according to the availability of berries.

Geese used scrublands most at the onset of the breeding season in October, during moulting in March and in September during summer flocking, reflecting different stages in the birds' annual cycle. Some of the observed distribution patterns were associated with variation in rainfall which, in turn, may have affected phenological patterns. The forage quality in one habitat relative to another may explain part of the variation in the observed distribution patterns, ie if food availability and quality in the grasslands are low, birds may move to scrublands and *vice versa.*

During this study, Hawaiian geese were seen feeding on Mamaki berries at Site 6, especially during the peak of the Mamaki fruiting period between July and October. Site 6 was created during the 1969 volcanic eruption of Mauna Ulu. Mamaki colonized the newly created cinder field and the first Hawaiian Goose nest was found six years after the eruption (H. Hoshide pers. comm.). Initially, Mamaki bushes were small (H. Hoshide pers. comm.) and could only support a small number of geese. The increase in goose numbers at Site 6 therefore might be due to two factors: firstly, bushes increasing in size were able to support more geese; secondly, the Hawaiian Goose population grew significantly between 1981 and 1995.

Fruit production was well synchronized in species like Mamaki, which may have allowed the geese to built up a tradition in exploiting these seasonally abundant food resources. In other species like Ohelo and Pukiawe, however, a large variation in fruiting patterns occurred. The temporal and spatial variability of berry abundance in these plants might be related to variation in rainfall between months, years and sites. Similar variation in phenology has been described by Bridges *et al.* (1981) for some Hawaiian tree species. Rainfall relationships are widely viewed as an important factor in determining the flowering and fruiting periods. The role of rainfall, however, is complex and not well understood (Bridges *et al.* 1981). In Hawaii, few studies have shown the climatological mechanisms involved in phenology, and even fewer studies have considered variation between years. The large variation in phenology observed in this study, highlights the need for more detailed and longer-term studies to investigate fully the effect of varying rainfall patterns on plant phenology.

Most Hawaiian Geese initiated nests in November when average rainfall was highest. However, few birds nested in January, which had the second highest average rainfall. Therefore, rainfall appears to explain only part of the observed nest initiation pattern.

Unlike in temperate and arctic nesting goose species, clutch size in Hawaiian Geese appeared to be independent of lay-date with no discernible trend throughout the breeding season (Barry 1962; Ryder 1972; Findlay & Cooke 1982). Clutch size in most bird species is affected by food availability. The more nutrient reserves a female can accumulate prior to laying, the larger her clutch. With extremely variable rainfall patterns throughout the breeding season, food availability may have been variable in consecutive years, which may explain the lack of a seasonal trend in clutch size.

Individual females varied their time of nesting between years. Some had a relatively narrow time window, while others changed lay date considerably. In terms of evolution this may represent different strategies. Several types (eg consistent or inconsistent) might survive in the population as a result of considerable annual and monthly variation between sites in environmental conditions before, during and after incubation.

In a wide range of bird species, early breeders tend to fledge more chicks (Daan *et al.* 1989; Rohwer 1992), and this observation is often associated with higher food availability earlier in the season. In Hawaii, Black *et al.* (1994) found a seasonal decline in food quality and density during the nesting and brood rearing season between November and January. During the study, the berry abundance of some important food plants, eg Pukiawe and Mamaki, declined throughout the season in some areas, but patterns varied between sites, years and species. Ohelo berries, for example, fluctuated throughout the year without any clear seasonal trend. In many cases, birds that nested earlier in the season were more successful, but other events such as predation and severe weather caused deviation from the predicted pattern. Breeding pairs compete for a limited amount of food, and not all pairs will be successful in securing a good territory (Black *et al.* 1994). Birds that nest early may be more successful because they defend better territories.

Vegetative growth in four plant species was lowest in April and May, which coincides with the end of the Hawaiian Goose breeding season. Young growth in plants is very nutritious and important for gosling growth. It is possible that the lack of vegetative growth in April limits the breeding season. Late broods rarely fledge and this may be due to the lack of nutritious food which allows growth.

In addition to differences in the phenology of food resources, local differences in predation pressure through introduced Indian Mongoose *Herpestes auropunctatus*, dogs, cats and pigs, are likely to have an effect on goose distribution and the timing of nesting. Effects of food phenology and predators are probably linked. For example, Capercaille *Tetrao urogallus* chicks have been shown to call more frequently when they are hungry, increasing the risk of being detected by a predator (D. Dugan pers. comm). Egg predation is also more likely to occur during times of low food availability (Prop *et al.* 1984). At such times, females may take breaks from incubation for longer periods in order to feed, and this leaves the nest unprotected (Banko 1988). Further studies on the interplay between food availability, abundance of small rodents and predators in relation to Hawaiian Goose productivity are needed.

Management implications

This study is a another step towards understanding the large ecological variations that Hawaiian Geese have to deal with in their annual cycle. The Hawaiian environment is less predictable than conditions in the arctic where many related species breed. This poses problems in the timing of management of this endangered species, as some measures taken, such as predator control, providing water or additional forage will be dependant on environmental conditions. Therefore, to fine-tune conservation measures, federal, state and private wildlife managers in Hawaii will have to be flexible in their work schedules.

Although Hawaiian Geese utilise disturbed grassland habitats and benefit from introduced plants as a food resource (Black *et al.* 1994; Woog & Black 2001), this paper highlights the importance of native plants in their diet. The restoration of disturbed habitats remains a long-term objective (Stone & Scott 1985), and when choosing plants for this purpose, Hawaiian Geese would benefit from native species such as Ohelo, Pukiawe, Mamaki and Uulei. The importance of the regularly-used feeding site at Kipuka Kahalii also became apparent during this study. The area is at high risk of destruction from a volcanic eruption of the close-by Mauna Ulu volcano, which is still active. Planting additional areas with Mamaki and other native plants in and around Hawaii Volcanoes National Park would lower the chances of all sites being lost through volcanic activity, and would secure additional forage for the endangered Hawaiian Geese.

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Appendix 1

Monthly range of rainfall (mm) at Hawaii Volcanoes National Park between 1988 and 1995.

	K. Nene *(850m)*	Ainahou *(920m)*	Halemaumau *(1,100m)*	Keamoku *(1,700m)*	Mauna Loa *(2,330m)*
January	37-705	68-778	23-640	42-612	37-488
February	9-416	12-492	9-410	9-240	2-430
March	5-440	41-574	19-485	3-159	4-473
April	20-199	60-190	28-180	21-252	27-252
May	4-63	54-168	16-157	18-134	26-160
June	0-39	39-87	7-64	6-87	7-94
July	6-367	65-395	22-335	18-363	24-389
August	13-164	33-403	24-217	32-155	35-312
September	45-495	40-531	28-430	38-164	38-261
October	40-562	78-575	28-343	13-287	15-355
November	27-826	37-1092	23-824	13-368	16-654
December	27-523	39-461	37-327	12-223	10-205

Appendix 2.
Monthly mean rainfall (mm) at Hawaii Volcanoes National Park between 1988 and 1995.

	K.Nene *(850m)*	Ainahou *(920m)*	Halemaumau *(1,100m)*	Keamoku *(1,700m)*	Mauna Loa *(2,330m)*
January	223	275	203	161	167
February	157	184	154	94	159
March	151	183	147	71	114
April	65	102	62	71	73
May	29	74	57	66	68
June	17	58	24	30	36
July	125	162	122	119	162
August	79	119	83	69	116
September	153	185	137	105	132
October	158	179	117	107	111
November	292	399	291	154	260
December	213	250	164	110	111

Appendix 3.
Monthly rainfall (mm) at Kipuka Nene between 1988 and 1995.

	1988	1989	1990	1991	1992	1993	1994	1995
January	58	316	705	131	37	225	69	111
February	21	284	350	62	23	9	416	28
March	107	440	39	364	5	40	184	30
April	20	199	61	66	74	24	21	57
May	35	54	4	7	63	30	13	25
June	0	39	15	9	30	10	25	7
July	6	349	57	44	75	367	63	42
August	112	81	28	133	78	24	164	13
September	45	61	161	183	171	47	495	57
October	274	562	71	117	84	69	40	45
November	331	40	826	181	506	27	218	205
December	156	62	354	375	523	33	27	173
Total	1,165	2,487	2,671	1,672	1,669	905	1,735	793

Appendix 4.
Average plant density per 100m² of species studied in eight scrubland study areas. Blackberries and *Rumex* at Site 2 were distributed in clumps and did not occur in the randomly chosen survey plots.

Site	1	2	3	4	5	6	7	8
Altitude (m)	*1,830*	*1,130*	*1,120*	*880*	*910*	*790*	*880*	*730*
Plots (100m²)	*(n=2)*	*(n=5)*	*(n=8)**	*(n=4)*	*(n=4)*	*(n=10)**	*(n=3)*	*(n=2)*
Food source: Berries								
Kukaenene	3.5	1.0	-	-	-	-	-	-
Uulei	-	-	-	-	13.0	-	1.0	-
Mamaki	-	-	-	-	-	0.75	-	-
Pukiawe	3.0	1.0	6.2	24.0	31.3	0.25	17.7	14.0
Ohelo	-	3.0	2.4	-	-	-	-	-
Food source: Leaves								
Buddleia	-	1.8	-	-	-	1.7	-	-
Rumex	-	n.a.	-	-	-	0.5	-	-
Pamakani	-	3.4	-	-	-	1.0	-	-
Dubautia	-	12.4	-	1.0	-	0.8	-	-

*Because of sparse vegetation cover 400m² were surveyed and then totals divided by four.