FOODS OF THE HAWAIIAN GOOSE

By PAUL H. BALDWIN

In a previous paper (Baldwin, 1945) the distribution and reduction in numbers of the Hawaiian Goose, or Nene (*Nesochen sandvicensis*), were described. In the present study, the food habits are considered as a step in the analysis of causes of the reduction of the population. Because of the practicability of obtaining material, this work is based mainly on the analysis of droppings.

We should attempt to learn whether or not food resources are a limiting factor in the success of the goose in its environment of today. Former writers have reported that seasonal changes in availability of food in the range of the Nene tend to cause it to shift about between uplands and lowlands at various seasons of the year. Also, availability of foods has been considered as decisive in influencing the area chosen for nesting.

The Hawaiian Goose is confined to the Island of Hawaii and inhabits barren lowland country from sea level to 3000 feet and upland slopes of the mountains, Mauna Loa and Hualalai, from 3000 to 9000 feet. Much of the range consists of barren lava flows which support only a scanty growth of herbs, ferns and shrubs and are entirely devoid of water. Other parts of the range include moist grasslands and open forests. The yearly rainfall in these areas falls between the probable limits of 15 and 120 inches. The lowland range is on the leeward side of the island, hence is hot and dry, whereas the upland range is more variable in climate.

The goose is a vegetarian, utilizing grasses, berries and herbs. The following plants have been mentioned by various authors as providing food: grasses, *Fragaria chiloensis* (white strawberry), *Rubus hawaiiensis* and *R. Macraei* (akala), *Vaccinium reticulatum* (ohelo), *Styphelia Tameiameiae* (pukiawe), *Solanum nodiflorum* (popolo), *Coprosma ernodeoides* (kukainene), and *Sonchus oleraceus* (sow thistle). It was agreed that the berries of *Vaccinium* are one of the most important foods. *Solanum* and *Sonchus* were also considered important.

The Nene went to the lower elevations in winter and spring to take advantage of the new growth of greens for rearing their young, according to Henshaw (1902:105). They returned to the uplands in summer where they fed on berries. Foods said to be abundant in the uplands in summer were grasses, *Vaccinium,* and other berries. These were less plentiful during the cold winter months. Abundant foods in the lowlands in winter were grasses, *Sonchus,* and other herbs. In spite of the scanty crop of berries in the uplands during winter, Peale (1848:250) found Nene subsisting on them in upland lava fields in November. In spring, grasses and *Sonchus* were said to continue abundant in the lowlands, and in late spring wild strawberries were obtainable in the mountains. In summer, strawberries continued to bear but went out of season around the end of July on Hualalai (Brigham, 1909:12). In the fall, berries of sorts were available.

Competition from grazing animals was thought by Pope (1932:110) to have been responsible for migration to the lowlands in winter, while Perkins pointed out that cattle destroy the strawberry plants in Nene range. Lamb (1937) suggested that pheasants are competitors of the Nene for foods.

Concerning differences between the food habits of the Nene and other species of geese, Miller (1937:3) points out that in comparison with winter flocks of geese in North America the Nene probably does less feeding on short grass and on grain growing on open level surfaces and appears to do no foraging in the mud at the edges of ponds and marshes.

The knowledge available as summarized above affords a meagre concept of the foods eaten. We find no detailed list of foods used, no mention of the chemical composition of foods or ecological aspects of the food supply. Nothing is said about the nutritional requirements of the geese themselves. In this study we attempt to supply some of this information, although the subject of the nutritional requirements of the geese could not be included.

Procedures.—Of 640 droppings collected, 543 were microscopically dissected. The material was gathered over a period of six years, between 1938 and 1944. In the field the droppings were readily recognizable. Except for some distinctly small droppings, presumably from juvenal birds, they were fairly uniform in size, and all were typically laminated at right angles to the long axis. A J-shape was characteristic. Mongoose droppings were similar in size but not in other features. Pheasant droppings were smaller, not laminated, and not frequently seen. The material varied from bleached to fresh.

Volumetric measurements of identified components were made by the water displacement method and by visual estimation. It proved possible to identify about 40 per cent of the material. Plant names used in the study are after Fagerlund and Mitchell (1944), and considerable data on the distribution of plants in Hawaii National Park were drawn from this work. The project was carried out on behalf of the United States National Park Service. The University of Hawaii kindly loaned a microscope for the work.

LIST OF FOODS

The following list of foods includes those actually identified in this study together with those attributed to the diet of the Nene by previous authors. A summary of foods actually found with data on the number of recorded occurrences, the per cent of occurrences, and the per cent of the total volume for each food is presented in table 1.

Agrostis avenacea. Grass.

Availability: Frequent along roadsides, Hawaii National Park (henceforth H. N. P.).

Use: Found in droppings from Kau Desert. Seeds, leaves, stems utilized.

Axonopus affinis. Narrow-leaved carpet-grass.

Availability: Abundant on grazed lands in Humuula (5800 ft.); abundant in moist pastures below 2000 ft. (Whitney, Hosaka, and Ripperton, 1939:26).

Use: Found in droppings from Humuula. Seeds, leaves, stems utilized.

Bidens.

Availability: Various species found from sea level to 7000 ft. on Mauna Loa in H. N. P.; greatest abundance in rather dry areas.

Use: Found in droppings from Mauna Loa in H. N. P. and Puuwaawaa. Seeds, leaves, stems utilized. Probably important in lowland areas.

Bulbostylis capillaris. Sedge.

Availability: Frequent on volcanic ash deposits in Kau Desert between 2000 and 4000 ft.

Use: Found in droppings from Kau Desert. A minute plant. Mainly seeds utilized.

Carex Macloviana. Sedge.

Availability: Frequent on slopes of Mauna Loa in H. N. P., from 4000 to 7000 ft.

Use: Found in droppings from Mauna Loa in H. N. P. and Humuula. Seeds utilized and probably the leaves also were frequently taken.

Carex wahuensis. Sedge.

Availability: Frequent in moderately wet areas in H. N. P. and occurring up to 10,000 feet on Mauna Loa; seen at summit of Hualalai.

Use: Found in droppings from Mauna Loa in H. N. P., Humuula, and summit of Hualalai. Seeds recovered and also green parts. Is one of the most important foods.

Carex. Sedge.

Use: Found in droppings from Humuula. Probably is *C. wahuensis,* but could not be specifically identified.

Cirsium vulgare. Common thistle.

Availability: Frequent in dry to moderately dry areas from the Kau Desert at 2000 to 6000 ft. on Mauna Loa in H. N. P.; found at summit of Hualalai and Puuwaawaa; where rainfall is less than 60 inches, at low and medium elevations.

Use: Found in only one dropping from Puuwaawaa. Seed feathers found. An important food.

Coprosma ernodeoides, var. *typica*. Kukainene.

Availability: Frequent in moderately wet areas from Kilauea up to about 8000 ft. on Mauna Loa in H. N. P.; abundant in Humuula; found at summit of Hualalai but not at lower elevations on Puuwaawaa where droppings were collected.

Use: Found in droppings from Mauna Loa in H. N. P. and Humuula. Fruits utilized. Perhaps not so important as previously thought.

Cyperus polystachyos. Sedge, kilioopu.

Availability: Abundant along roads and trails at Kilauea; frequent in Kau Desert; common in low altitude and occasional in medium altitude zones in Hawaii where rainfall is over 60 inches per year (Ripperton and Hosaka, 1942:48).

Use: Found only in droppings from the Kau Desert. Seeds and green parts utilized.

Deschampsia nubigena. Grass.

Availability: Frequent along roadsides about Kilauea and dominant on Mauna Loa slopes from 4000 to 7000 ft.; seen around 8000 ft. on Hualalai.

Use: Found in droppings from Mauna Loa (H. N. P., Humuula) and summit of Hualalai. Seeds, leaves, stems utilized. An important food.

Digitaria pruriens. Crabgrass.

Availability: Infrequent in moderately dry areas in H. N. P.: rather abundant on all the Hawaiian Islands in wet regions of the lowlands (Whitney, Hosaka, and Ripperton, 1939:54).

Use: Found in droppings from Kau Desert and abundantly in droppings from Puuwaawaa. Seeds and green parts utilized.

Digitaria violascens. Crabgrass.

Availability: Frequent in moderately dry areas in H. N. P.; fairly abundant in moist and semi-dry regions to an altitude of 5000 ft. or more (Whitney, Hosaka, and Ripperton, 1939:57).

Use: Found in droppings from Kau Desert (abundantly) and from Mauna Loa in H. N. P., Puuwaawaa, and Humuula. Seeds especially recovered, but green parts also found. An important food.

Festuca megalura. Foxtail fescue.

Availability: Of restricted occurrence in H. N. P. around 4000 ft.; found occasionally at medium altitudes in moist situations (Whitney, Hosaka, and Ripperton, 1939:72).

Use: Found in droppings from Mauna Loa in H. N. P. Seeds and green parts utilized.

Fragaria chiloensis. White strawberry.

Availability: Frequent in moderately wet forests of medium elevation; in H. N. P. found from perhaps 3000 to 6000 ft., abundant around 4000.

Use: Not recovered from droppings. Fruits utilized, according to various authors.

Gnaphalium sandwicensium. Enaena.

Availability: Frequent in Kau Desert, also found on Mauna Loa in H. N. P. at 9000 ft.; found at summit of Hualalai; generally rare up to 4000 ft. in areas where rainfall is 40 to 60 inches (Ripperton and Hosaka, 1942:53).

Use: Found in droppings from Mauna Loa in H. N. P. and from summit of Hualalai. Leaves and flowers eaten. Perhaps important food at times.

Hypochaeris radicata. Gosmore.

Availability: Frequent to abundant in moderately dry areas from 2000 to 9500 ft. in H. N. P.; found at summit of Hualalai and at Puuwaawaa; generally common from 2500 to 7000 ft. where the rainfall is 40 to 60 inches or less and rare to occasional where the rainfall is more than 60 inches (Ripperton and Hosaka, 1942:53).

Use: Found abundantly in droppings from Mauna Loa in H. N. P. and from Humuula and Puuwaawaa. Seeds, leaves, stems, flowers utilized. Most important herb.

Luzula campestris. Rush.

Availability: Frequent around Kilauea and on Mauna Loa slope in H. N. P.

Use: Found in a single dropping from 7500 ft. on Mauna Loa. Only one seed covering was seen. An available but little utilized plant.

Oxalis corniculata. Lady's sorrel.

Availability: Frequent at Kilauea and rare on Mauna Loa in H. N. P. at 6250 ft.; rare at elevations from 2500 to 3000 ft., with rainfall of 20 to 40 inches, common in areas less than 2500 ft., rainfall 40 to 60 inches (Ripperton and Hosaka, 1942:54).

Use: Found in droppings from Mauna Loa in H. N. P. and from Puuwaawaa. Traces of seeds only.

Panicum tenuifolium. Mountain pili.

Availability: Frequent on Mauna Loa in H. N. P.; abundant at high altitudes on the island of Hawaii and able to grow in rather dry, windswept areas, where soil is rocky and shallow (Whitney, Hosaka, and Ripperton, 1939:91).

Use: Found in droppings from Mauna Loa in H. N. P. and from Humuula. Seeds and green parts utilized.

Physalis peruviana. Cape gooseberry, poha.

Availability: Infrequent from 4000 to 6000 ft. in H. N. P.; frequent at lower elevations in areas of about 30 to 60 inches of rainfall.

Use: Not recovered in droppings. As described later, a foraging Nene seemed to take something from poha vines.

Rubus hawaiiensis and *R. Macraei.* Hawaiian raspberry, akala.

Availability: Common to occasional in moderately wet to wet areas from 4000 to 7000 ft.; infrequent in H. N. P. on Mauna Loa slope from 4200 to 6500 ft.; seen at Puuwaawaa.

Use: Not found in droppings. These two species are listed as berry food plants by Pope (1932:110).

Rubus rosaefolius. Thimbleberry.

Availability: Frequent and widespread in wet and moderately wet forests and open grassy areas from sea level to 7000 ft., but not common above 5000 ft. in H. N. P. Only available in wettest parts of the Nene range.

Use: Found in droppings from Puuwaawaa. Fruits utilized.

Rumex acetosella. Sheep sorrel.

Availability: Frequent and widespread in H. N. P.; common in areas at elevations of 2500 to 4000 ft., and a rainfall of 40 to 60 inches (Ripperton and Hosaka, 1942:54).

Use: Found in droppings from Mauna Loa in H. N. P. and from Humuula. Mostly seeds found in droppings.

Silene gallica. Small-flowered catchfly.

Availability: Rare in moderately dry areas between 2000 and 3000 ft. in H. N. P.

Use: Found in droppings from Mauna Loa in H. N. P. and from the Kau Desert. Only seed cases showed up in the droppings. The number of occurrences was high (table 1).

Sisyrinchium acre. Mauulaili.

Availability: Frequent on Mauna Loa in H. N. P. around 6000 ft.; occasional to common from 4000 to 10,000 ft. in areas having 50 inches of rain or less and occasional in areas from 4000 to less than 7000 having 60 or more inches of rain (Ripperton and Hosaka, 1942:52).

Use: Found only in one dropping from 6250 ft., Mauna Loa in H. N. P. Several seeds were present. An available but unimportant food.

Solanum nodiflorum. Popolo.

Availability: Frequent from sea level to 4000 ft., and infrequent at higher elevations in dry to moderately wet areas in H. N. P.; not seen by the author at other upland places where droppings were collected but said to be common at elevations less than 2500 ft. where rainfall is 40 to 60 inches, and occasional up to 3000 ft. where the rainfall is 20 to 40 inches (Ripperton and Hosaka, 1942:55).

Use: Found in droppings from Mauna Loa in H. N. P. and Puuwaawaa. Seeds and skins of fruits recovered, indicating use of fruits. An important food.

Sonchus oleraceus. Sow thistle, pualele.

Availability: Common from sea level to 3000 ft, where the rainfall is less than 60 inches; occasional below 1500 ft. where rainfall is over 60 inches; in H. N. P. infrequent to frequent in moderately wet to dry areas from sea level to 4000 ft., rare up to 6250 ft.; absent from summit of Hualalai and Puuwaawaa at 4000 ft., where the writer collected droppings.

Use: Not found in droppings. Previously considered an important food plant. It undoubtedly is an important food plant in the lowlands, but apparently is not in the uplands because of low availability.

Sporobolis capensis. Rattail grass.

Availability: Abundant along roads and on grazed land in H. N. P.; seen at Puuwaawaa and Humuula; has become dominant over some of the range land in cool, moist areas and is abundant in open pasture land from low to medium altitudes (Whitney, Hosaka, and Ripperton, 1939:115).

Use: Found only in droppings from Puuwaawaa. Seeds only recovered from droppings. Although highly available, this grass seems to be rejected for the most part.

Styphelia Douglasii. Pukeawe.

Availability: Frequent to abundant on Mauna Loa at about 9000 ft.

Use: Found in droppings from Mauna Loa in H. N. P. Pits and leaves found. Indistinguishable from the following species in the droppings, except by leaf characters, so probably occurred more than recorded.

Styphelia Tameiameiae. Pukeawe.

Availability: Frequent to abundant from 2000 to 9000 ft. in H. N. P. in dry desert areas to moderately wet forests; characteristically in zones of rainfall of 40 to 60 inches per year or less (Ripperton and Hosaka, 1942:55).

Use: Found in droppings from Mauna Loa in H. N. P., Kau Desert and summit of Hualalai. Pits of fruit recovered almost entirely, indicating consumption of fruits. An important plant.

Vaccinium reticulatum. Ohelo.

Availability: Frequent to abundant from about 2800 to 8000 ft. in H. N. P. (Kau Desert, Kilauea, Mauna Loa); frequent on Mauna Loa lava flows in Humuula; frequent at summit of Hualalai and in saddle between Hualalai and Mauna Loa; generally absent below 2500 ft. A related species, *V. peleanum*, is abundant on Mauna Loa in H. N. P. from 8000 to 10,000 ft. and is probably indistinguishable from *V. reticulatum* in the droppings. Found in areas where rainfall is 30 to 60 inches per year.

Use: Found in droppings from Mauna Loa in H. N. P., Kau Desert, and the summit of Hualalai. Fruits utilized. An important food.

Verbena litoralis. Verbena.

Availability: Frequent about Kilauea and the middle slopes of Mauna Loa in H. N. P.; frequent in Humuula and at Puuwaawaa around 4000 ft.; occasional to common up to 6000 ft., where the rainfall is 20 to 60 inches per year.

Use: Found in droppings from Mauna Loa in H. N. P., Humuula, and Puuwaawaa. Seeds and green parts taken. A little used plant in view of its availability.

Moss.

Moss may or may not have been ingested by the goose. In some cases it was found growing on the droppings. Traces only found.

Lichen.

Lichens growing on lava rock frequently adhered to the droppings. In most cases they were ingested, however, as they were found within the droppings. Traces only found.

Arthropoda.

In two instances single fragments of arthropods were found. These may have been ingested accidentally with greens, fruits, or with clusters of seeds. In one case ohelo fruits were also present and in the other case, seeds, fruits, and leaves were present in the dropping. Animal life seems to play no part in the food habits of the adult goose as revealed in this study.

Chemical composition of the foods.—Eight of the more important foods were selected for chemical analysis in order that a more complete interpretation of the feeding habits of the Nene could be made. We are indebted to the staff of the laboratories of the Hawaii Agricultural Experiment Station at the University of Hawaii for performing the analyses. The proximate composition was determined by the Chemistry and Soils Department and the minerals and vitamins by the Nutrition Department.

Fresh samples of the foods in five-pound lots were sent to the laboratories in Honolulu via air express from Hilo, Hawaii. The foods were kept as cool as possible during the two days which elapsed between the picking and the start of the analyses. The name, date collected, source and part analyzed of each plant food is given in table 2.

Grass seeds are commonly broken up in the droppings, indicating utilization of the starchy and proteinaceous contents. Although *Deschampsia nubigena* and *Digitaria* were significant sources of grain among the grasses, they could not be obtained for analysis. *Carex wahuensis* with its rather large seed heads was important among the sedges, and the seeds were relatively rich in crude protein, fat (ether extract), and carbohydrate. They were also high in riboflavin and moderately so in thiamine. The values for these constituents are presented in table 3. *Hypochaeris radicata* and *Bidens* were the herbs whose seeds were most used. The seeds of the former were higher in calcium and phosphorous than any of the other principle foods analyzed. They were also moderately high in thiamine and riboflavin.

The most frequently recorded pulpy fruits were *Vaccinium reticulatum* and *Solanum nodiflorum*, which are juicy and have small seeds. The former was lowest in proteins, carbohydrates, crude fiber, ash, calcium, and phosphorous of all the foods tested. It was also very low in thiamine and riboflavin but very high in moisture content.

Table 1

Foods Found in 543 Hawaiian Goose Droppings

Name	Number of occurrences	Per cent of occurrences	Per cent of total volume	Average volume per individual dropping in per cent
Gramineae				
Agrostis avenacea	30	6	1.5	28
Axonopus affinis (narrow-leaved carpet-grass)	10	2	1.8	98
Deschampsia nubigena	111	20	8.3	41
Digitaria pruriens (crabgrass)	25	5	2.3	49
Digitaria violascens (crabgrass)	58	11	3.9	37
Festuca megalura (foxtail fescue)	16	3	0.9	32
Panicum tenuifolium (mountain pili)	31	6	1.3	23
Sporobolis capensis (rattail grass)	6	1	0.1	10
Cyperaceae				
Bulbostylis capillaris (sedge)	13	2	0.4	16
Carex Macloviana (sedge)	29	5	1.0	19
Carex wahuensis (sedge)	49	9	3.2	35
Carex	6	1	0.5	45
Cyperus polystachyos (sedge, kilioopu)	6	1	0.4	37
Juncaceae				
Luzula campestris (rush)	1	0.2	Tr.	....
Iridaceae				
Sisyrinchium acre (mauulaili)	1	0.2	Tr.	....
Polygonaceae				
Rumex acetosella (sheep sorrel)	23	4	0.5	12
Caryophyllaceae				
Silene gallica (small-flowered catchfly)	58	11	0.2	2
Rosaceae				
Rubus rosaefolius (thimbleberry)	32	6	1.3	22
Oxalidaceae				
Oxalis corniculata (lady's sorrel)	3	0.6	Tr.	....
Ericaceae				
Vaccinium reticulatum (ohelo)	83	15	1.6	11
Epacridaceae				
Styphelia Douglasii (pukeawe)	3[1]	0.6	Tr.	2
Styphelia Tameiameiae (pukeawe)	121	22	3.2	17
Verbenaceae				
Verbena litoralis (verbena)	17	3	0.2	5
Solanaceae				
Solanum nodiflorum (popolo)	51	9	1.5	6
Rubiaceae				
Coprosma ernodeoides (kukainene)	28	5	0.6	12
Compositae				
Bidens	14	3	1.7	68
Cirsium vulgare (common thistle)	1	0.2	Tr.	....
Gnaphalium sandwicensium (enaena)	4	0.7	0.3	38
Hypochaeris radicata (gosmore)	84	15	7.0	45
Unidentified plants				
Grass seed(?)	2	0.4	0.4	
Reddish seed	3	0.6	Tr.	
Moss	22	4	Tr.	
Lichen	12	2	Tr.	
Arthropoda	2	0.4	Tr.	
Unrecognizable remains	....	....	55.9	
Identifiable remains	....	....	44.1	

[1] See text, this species.

Table 2

Sources of Foods of the Hawaiian Goose Analyzed for Composition

Name	Date collected	Locality	Part analyzed
Carex wahuensis	Jan. 6, 1946	H. N. P., Mauna Loa, 4500-6000 ft.	whole fruits
Coprosma ernodeoides	Nov. 4, 1945	H. N. P., Mauna Loa, 5000-6000 ft.	whole fruits
Deschampsia nubigena	Oct. 21, 1945	H. N. P., Mauna Loa, 5000 ft.	green leaves
Hypochaeris radicata	Dec. 16, 1945	H. N. P., Mauna Loa, 4000-6000 ft.	green leaves
Hypochaeris radicata	Nov. 18, 1945	H. N. P., Mauna Loa, 4000-6000 ft.	seed heads
Rubus rosaefolius	Jan. 20, 1946	H. N. P., Mauna Loa, 4000 ft.	whole fruits
Styphelia Tameiameiae	Dec. 2, 1945	H. N. P., Mauna Loa, 5000 ft.	whole fruits
Vaccinium reticulatum	Oct. 8, 1945	H. N. P., Kilauea Crater, 4000 ft.	whole fruits

Table 3

Chemical Composition of Some Foods Eaten by the Hawaiian Goose

Name	Moisture	Protein N×6.25	Ether Extract	Carbohydrate (by difference)	Crude Fiber	Ash	Ca	P	Thiamine mcg/100 gm.	Riboflavin mcg/100 gm.
Carex wahuensis. Seeds.	48.0	3.7	3.0	29.7	14.0	1.6	.048	.056	78	130
Coprosma ernodeoides. Fruits.	91.0	0.4	0.6	5.8	1.8	0.4	.026	.013	20	too low to measure
Deschampsia nubigena. Greens.	43.9	3.9	1.25	28.7	18.0	4.2	.077	.049	128	152
Hypochaeris radicata. Seed heads.	.....	.....	.....	.....	.....	1.8	.243	.078	63	100
Hypochaeris radicata. Greens.	87.9	1.7	0.70	6.2	1.75	1.7	.222	.043	30	140
Rubus rosaefolius. Fruits.	81.3	1.25	2.36	10.0	4.32	0.75	.032	.051	20	25
Styphelia Tameiameiae. Fruits.	30.2	1.7	6.7	34.1	26.6	0.7	.145	.014	16	too low to measure
Vaccinium reticulatum. Fruits.	92.8	0.25	1.1	4.9	0.75	0.2	.019	.009	.16	less than 10

Coprosma ernodeoides has purple juicy fruits with large central seeds. These also are high in moisture but relatively low in all other substances. Presumably these juicy fruits are important in furnishing water on the dry mountain slopes of the Nene range. *Rubus rosaefolius* proved rather high in ether extract and richer in crude protein, carbohydrate, crude fiber, ash, calcium, phosphorous and riboflavin than the fruits just mentioned. *Styphelia Tameiameiae* is a shrub with an abundance of small pithy fruits with a central pit which were frequently encountered in the droppings. They probably serve as a grinding agent in the gizzard. The fruits were the lowest in moisture of all types tested, but they were the highest in carbohydrate, ether extract and crude fiber. They were moderately high in calcium.

Greens consisting of leaves, stems, and flowers form the bulkiest component of the diet of the goose. Both grasses and herbs provide large amounts of this material. Among the grasses, *Deschampsia nubigena* and *Digitaria* were of highest occurrence and volume in the droppings. The green leaves of the herb *Hypochaeris radicata* were much higher in moisture than the leaves of *D. nubigena,* although it is difficult to know how closely the moisture content of these foods should be compared because of unavoidable differences in treatment between the time the greens were picked and analyzed. The leaves of *H. radicata* were next highest to the seed heads of the same plant in calcium. This abundant herb apparently serves to supply a large proportion of the calcium consumed

by the goose. In the Hawaii National Park, pheasants (*Phasianus colchicus*) and quail (*Lophortyx californica*) were also found to eat quantities of this plant.

Apparently grass greens supply a large portion of the proteins, although grain and seeds may prove to furnish large amounts when they are available. Crude fiber passes through the digestive tract in large quantities. Most of the foods appeared relatively low in phosphorous.

Foods in the environment.—Grass stands out as a more important food item than herbs or shrubs both by number of occurrences and volume (table 4). However, many greens were unrecognizable as to species and many probably represented some of the herbs. Ferns of many species are present in the environment of the Nene, but if taken they did not show up in the droppings. Most of the fruits consumed come from plants

Table 4

Plant Habit Groups Found in 543 Droppings

Habit	Number of occurrences	Per cent of identified plant items	Per cent of total volume of 543 droppings
Grasses and sedges	401	43	25.6
Herbs	256	28	11.4
Shrubs	267	29	6.7

of shrubby habit, although some were from herbs. Trees contributed no food items identified, although some seeds may be ingested occasionally and tender growth from seedlings may be eaten.

Most of the important food plants grow in moderately wet areas (table 5). This accords with what would be expected, for the greater part of the Nene range occurs in the moderately wet regions.

The plants utilized as found in the droppings are only a portion of the plants available in any of the areas studied, usually not more than half, as shown by lists of plants made in the vicinities where droppings were collected. Invariably the droppings showed some plants that could not be found by the author, indicating that the geese must feed in several spots within short periods. This is corroborated by observations that the Nene fly about over a number of square miles during any one day.

There is nothing to indicate that any particular food plant especially attracts the Nene in all regions. None plays the role of a limiting factor. The Nene occupies a zone where a variety of foods is obtainable, where the vegetation is an open forest or grassland or brush, and here the climate is dry to rather wet but for the most part with not over 80 inches of rainfall per year. This bird avoids the closed, humid forest of lowland and upland alike.

The upland habitat of Mauna Loa and Hualalai is characterized by land either covered with a thin soil layer or without continuous soil cover. In general, the former supports grassland and the latter shrub. New Mauna Loa lava flows are invaded by shrubs, mainly *Vaccinium* and *Styphelia,* the speed of invasion depending mainly upon climate but also upon surface characteristics of the lava. The Nene utilize plants found in all upland vegetative types except deep, wet forest and the sparse moss-lichen growth of alpine and recent lava flows.

The porous condition of lava precludes the holding of water at the surface in lakes or streams, hence the dryness of the general environment. In the relatively restricted areas where volcanic ash forms a surface layer more impervious to water, deeper soil, rain pools and a more mesophytic vegetation are found. Mesophytic grassland is doubt-

less more favorable habitat for the Nene than the dry lava. The Ainahou Kipuka in Humuula frequently has temporary rain pools, and to these the Nene come probably to feed at the edges. No community of aquatic vegetation has developed, but only moisture-tolerant terrestrial plants occur there.

The lowland habitat of Hualalai, Kilauea, Mauna Loa, and western Kohala is likewise characterized by vast areas of naked, porous lava, as well as much more restricted areas of volcanic ash with continuous soil cover. Ranching activities are carried out on the grasslands. While the almost barren lava flats near the sea are available to the Nene

Table 5

Food Plants Classified in Relation to Rainfall

Dry areas (15-40 inches)	Moderately wet areas (40-60 inches)	Wet areas (over 60 inches)
Bidens	*Carex wahuensis*	*Axonopus affinis*
Bulbostylis capillaris	*Coprosma ernodeoides*	*Cyperus polystachyos*
Gnaphalium sandwicensium	*Cyperus polystachyos*	*Digitaria violascens*
Panicum tenuifolium	*Deschampsia nubigena*	*Rubus rosaefolius*
Solanum nodiflorum	*Digitaria violascens*	
Sonchus oleraceus	*Fragaria chiloensis*	
Styphelia Tameiameiae	*Gnaphalium sandwicensium*	
Vaccinium reticulatum	*Hypochaeris radicata*	
	Rubus rosaefolius	
	Solanum nodiflorum	
	Sonchus oleraceus	
	Styphelia Tameiameiae	
	Vaccinium reticulatum	

in North Kona, they probably lack an abundance of green foods in the dry periods, which tend to occur in summer months. Wild grains, however, may be available during the summer dry periods in the lowlands.

Grassland vegetation is modified by ranching use both by cattle grazing and the introduction of grasses and pasture weeds. Many of the introduced grasses and herbs are utilized by the Nene as food, so the changes may not be deleterious as far as food supply is concerned, except in overgrazed areas where vegetation tends to be destroyed. The details of vegetative changes following severe overgrazing of upland pastures are not completely known, but if soil cover is lost and shrubs tend to enter, it is likely that the shrubs themselves will be a source of food to the Nene. It appears that food is not likely to be limiting in upland areas.

Since several of the most utilized plants, such as *Deschampsia, Vaccinium,* and *Styphelia,* are dominants in upland vegetational groups, the Nene is well adjusted to food potentialities in the upland environment of grassland and alpine shrub.

Most of the plants respond to seasonal climatic conditions and grow more vigorously during the summer in the uplands. However, berry-bearing shrubs such as *Vaccinium, Styphelia,* and *Rubus rosaefolius* have some fruit the year around, although the quantity varies seasonally. Certain shrubs are more rigorously seasonal, such as *Rubus hawaiiensis,* which bears fruit only in early summer on Mauna Loa in the park. Seasonal data on *Solanum* is lacking. Greens and fruits and seeds are to a degree seasonal in occurrence, but they are never totally lacking even on the higher slopes of Mauna Loa, as they might be if they were covered by deep snow. This does not happen, as snow seldom falls below 7500 feet.

On the hot, dry lower flanks of leeward Mauna Loa, just above sea level, abundant fresh green growth is practically limited to times of rainy weather. This is true on the South Kona coast and probably equally true on the North Kona coast. Seasonal effects

may be more pronounced in their influence on the abundance of Nene food here than in the uplands. It would be natural that a persecuted remnant population would retreat to the uplands rather than the lowlands, because of the scarcity of suitable foods in the hot dry lowlands during the dry seasons, whereas foods are available throughout the year in the uplands regardless of weather. Food factors appear likely to have influenced distribution somewhat during the recent period of range reduction by offering a more continuous supply of food plants throughout the year in the uplands than in the lowlands, although other non-food factors may have been more important. There seems to be no direct causative connection between any changes in food supply and the general decrease of the Nene during the past century, as all indications are that the food supply is adequate in quality and more than adequate in quantity over large areas of the Nene range.

Droppings from the Koa Oasis represented the dry Kau desert. On January 15, 1944, 13 species of plants of all habits were found growing there. Four of these were recovered in the droppings, and in addition the droppings contained remains of four species not found at the oasis. Two of the species, *Bulbostylis* and *Agrostis,* which grew there and were prominent in the droppings from the oasis were not found in droppings from other areas.

Droppings from Hawaii National Park above 4000 feet represented the moderately wet slopes of Mauna Loa. Plants collected from 3-trees kipuka (6250 ft.) numbered 36, while other species growing nearby added up to a total of 45. The number would be larger if plants of higher altitudes were to be included. In droppings from 3-trees kipuka 19 species were identified, of which 14 were plants found growing in the kipuka. It was evident that some choice of food plants was made from among those present on the Mauna Loa slopes, suggesting that the greater the number of types of plants there are present the more the element of choice enters into a determination of the Nene diet.

Droppings from the vicinity of Aina Hou represented the wet grasslands of Humuula. The moisture-tolerant *Axonopus affinis* was prominent in the droppings and, where the Nene had been feeding on nearby lava flows, native grasses, sedges, and fruits were conspicuous. Again it is evident that the goose is independent of any particular species of plant and utilizes various plants as they may offer food resources.

Droppings from the summit of Hualalai illustrate a habitat similar to the upper slopes of Mauna Loa above the grasslands. Of 27 species of plants seen there, only 6 appeared in the droppings, and most prominent among these were *Carex wahuensis, Styphelia Tameiameiae, Deschampsia* and *Vaccinium reticulatum,* indicating either selection or that the droppings represent food ingested elsewhere. The occurrence of *Gnaphalium sandwicensium* seems to indicate local feeding here, however.

Collections from the vicinity of Poohohoo represent the Puuwaawaa area of medium altitude in a rather wet belt. It is probable, however, that foods from the dry areas of lower elevations to the south were represented in the droppings. Forty-one kinds of grasses and herbs were listed for this general area, and only three of these were identified in the droppings. Four additional species of lowland and medium altitude identified in the droppings could not be found growing in the areas searched. This again suggests feeding in various areas within short periods of time as the geese fly about in the course of a day.

Similarity of food taken by possible competitors.—California Quail (*Lophortyx californica*). The range of the California Quail partly overlaps that of the Nene, as it is found in dry to moderately wet areas of sparse forest and grassland. In Hawaii National Park it occurs from about 2000 to 7000 feet. Fourteen quail stomachs from Hawaii National Park showed the following items in significant amounts: *Hypochaeris radicata*

(gosmore), seeds, leaves, flowers; *Carex wahuensis* (sedge), seeds; Gramineae (grass), seeds; Arthropoda; Mollusca.

The quail draws on the same foods as the Nene in the vegetable kingdom, although there may be a relatively higher usage of grains and seeds and lower usage of greens. Their niches obviously do not coincide but are somewhat related. The quail takes more animal matter. Does "competition" exist between the two species? Reactions between them on account of this overlap of range and food habits are undemonstrated. The numbers of individuals involved are small, for in the Nene the rather extensive range is far from saturated, and in the quail, extensive areas inhabited by the Nene support a relatively low quail population.

Pheasant (*Phasianus colchicus*). More than one variety or subspecies of pheasant occur side by side in the national park and elsewhere on Hawaii. The pheasant range probably overlaps the Nene range to a greater degree than does that of the California Quail, as it includes wet and rather thickly forested areas as well as the dry and moderately wet belt, sparse forests and grasslands. Twelve stomachs from Hawaii National Park showed the following foods as important: *Styphelia Tameiameiae* (pukeawe), fruits; *Hypochaeris radicata* (gosmore), seeds, leaves, flower buds; *Rubus rosaefolius* (thimbleberry), fruit; *Vaccinium reticulatum* (ohelo), fruits; *Coprosma ernodeoides* (kukainene), fruits; *Carex wahuensis* (sedge), seeds; Arthropoda; Mollusca.

These foods correspond even more closely with Nene foods than do those of the quail. However, the same considerations concerning competition apply here as in the former case. Under present conditions it is entirely likely that the pheasant exerts no depressing influence upon the Nene in respect to foods.

Peafowl (*Pavo cristatus*). The peafowl is naturalized in the Puuwaawaa area on the slope of Hualalai from about 2500 to 4000 feet. It inhabits the rather open forest and the borders of the pastures. It roosts in trees at night and forages in the fields in the early morning, retiring to cover during the day. We have no information on its foods. No interaction between the peafowl and the Nene was observed during field work at Puuwaawaa, and it seems unlikely that this fowl has any adverse effect upon the Nene under present conditions.

Turkey (*Meleagris gallopavo*). So few wild turkeys now remain on the ranges that they need not be considered a competitor. A few were seen at Puuwaawaa.

Guinea fowl (*Numida meleagris*). This bird does not naturalize extensively but is seen in small flocks on a few of the ranches, as on Mauna Loa near Keawewai. Certainly it is not a competitor in any practical sense under present conditions.

Geese. Several species of wild geese come to the Hawaiian Islands as winter visitants and may associate with the Nene at shore ponds in the lowlands. White-fronted Geese (?) were once seen feeding in vegetation in shallow water at Lanihau in North Kona. The numbers seem too small to allow of effective competition.

Goats. Under conditions of heavy goat browsing on limited areas, a great reduction in availability of food occurs, as seen at 3-trees kipuka, Hawaii National Park, from 1941 to 1946. The Nene would probably not linger for long at one of these depleted spots, but would fly on to other localities. Under light goat browsing, the plant food supply appears to remain adequate. In an indirect sense, goats exert an influence upon the Nene through modification of the soils and plants over a long period of time. It is likely that the soil losses in the dry sections of the national park in Kau are largely a result of heavy goat usage with destruction of the plant cover (Fagerlund and Mitchell, 1944:13).

Sheep. Bands of sheep reduce vegetation to a minimum on the barren slopes of

Mauna Loa facing Mauna Kea and Hualalai. It is likely that Nene are somewhat affected by pressure of sheep browsing.

Cattle. Wild cattle inhabit inaccessible forests, but under present conditions are probably less important as depressors of vegetation than sheep and goats.

Feeding behavior.—On November 28, 1941, the following observation was made between 2:45-4:30 p.m. at 3-trees kipuka: I found one Nene here and collected droppings which were scattered well over the kipuka, though thinly. The Nene was below the second tree and honked when it saw me. I froze, slowly retreated from sight in the lava channel about twenty yards below the goose and then stalked as close as possible, watching it forage in the weeds. It plucked gosmore (*Hypochaeris radicata*) flowers and swallowed them and also portions of the stems. It often turned its head and plucked a flower or seed head by the stem with the head hanging from the side of its mouth. There it stayed until it opened its bill to feed again or honk, when the food would drop out. I saw it crop about five flowers in 2 or 3 seconds. It also seemed to take something from poha (*Physalis peruviana*) vines. It spent much more time looking around than eating (it was aware that I had seen it but presumably didn't know I had stalked closer); its crop was bulging. It gave extended groans often and occasionally series of shrill high squawks. Twice it stretched up and flapped its wings. It walked around slowly among the weeds now and then but mostly stood still. Twice it went up on a look-out rock and watched for 10 or more minutes.

The Nene seems to pluck more than to peck, getting most of its food directly off the plant rather than probing on the ground for grains.

Feeding of captive Nene.—Nene are said to be easy to maintain in captivity if some of their psychological requirements are met, which will not concern us here. A few experiences on record teach us a little about food requirements, although no systematic experimentation has been conducted to our knowledge. One owner of a flock kept his birds in a large enclosed area where they had access to a brackish water pond and marsh vegetation. These birds ate quantities of napier grass (*Pennisetum purpureum*) and were fed grain twice a day. When breeding, they were removed to pens, where the young were raised in their early stages. In one year about a half dozen young in the downy stage died, and the owner attributed it to lack of sufficient lettuce (greens), and confinement for too long a period following hatching. The young in this flock in other years died frequently after reaching an age of about two months, the cause undetermined.

Another owner had a small flock confined in an enclosure 60 by 60 feet in the hot, dry lowlands. A small brackish water pond too small for swimming was within the enclosure, and a few grasses and weeds managed to survive. These birds were fed mainly on wheat supplemented with fresh cabbage and lettuce when available or with succulent greens and grasses in small amounts. It appeared that there were periods of days when no greens were available. These birds had never bred successfully in this enclosure. On the few occasions when eggs were laid, they were abandoned after a few days of incubation. Several factors were probably unfavorable in this situation, but it is possible that some dietary deficiency was mainly responsible for the lack of reproductive vigor.

SUMMARY

The Hawaiian Goose is a vegetarian subsisting on greens, fruits and grains. Thirty-one plant foods were identified through analysis of 543 droppings. The plants represented grow in areas which receive between 15 and 120 inches of rainfall per year and which lie between sea level and 9000 feet elevation. During hot dry seasons green food is scarce in the parts of the range on the leeward side of the island of Hawaii near sea

level, whereas during all seasons of the year a variety of foods is available at higher elevations. The goose is not dependent on any one food but tends to utilize plants which are abundant in any particular locality. This is illustrated by examples of the foods used at several localities.

The greater availability of food in the interior uplands may have favored the retreat of the remnant population of the goose to the uplands rather than to the lowlands.

The similarity of the food habits of possible competitors is discussed.

An example of the feeding behavior of the Hawaiian Goose is described.

The failure of captive birds to breed and the loss of young hatched in captivity may have been due to inadequate foods.

Data on the chemical composition of eight foods are presented.

ACKNOWLEDGEMENTS

The author gratefully acknowledges the work of Arthur L. Mitchell, who assisted extensively with the laboratory analyses and identified the plant remains.

LITERATURE CITED

Baldwin, P. H.
1945. The Hawaiian goose, its distribution and reduction in numbers. Condor, 47:27-37.
Brigham, W. T.
1909. The volcanoes of Kilauea and Mauna Loa. B. P. Bishop Mus., Mem. 11, No. 4, vii + 222 pp.
Fagerlund, G. O., and Mitchell, A. L.
1944. A checklist of the plants, Hawaii National Park, etc. Hawaii Nat. Park Nat. Hist. Bull. No. 9, Mimeo., 76 pp.
Henshaw, H. W.
1902. Birds of the Hawaiian Islands, etc. (Honolulu, Thos. G. Thrum), 146 pp.
Lamb, S. H.
1937. The nene in Hawaii. Hawaii National Park MS., 4 pp.
Miller, A. H.
1937. Structural modifications in the Hawaiian goose (*Nesochen sandvicensis*), a study in adaptive evolution. Univ. Calif. Publ. Zool., 42:1-80.
Peale, T. R.
1848. Mammalia and ornithology. U. S. Expl. Exped., 8:i-xxv + 17-338.
Pope, W. T.
1932. The Hawaiian goose or nene. Hawaiian Annual for 1933:107-112.
Ripperton, J. C., and Hosaka, E. Y.
1942. Vegetation zones of Hawaii. Hawaii Agr. Exper. Sta. Bull. 89, 60 pp.
Whitney, L. D., Hosaka, E. Y., and Ripperton, J. C.
1939. Grasses of the Hawaiian ranges. Hawaii Agr. Exper. Sta. Bull. 82, 148 pp.

Berkeley, California, March 1, 1947.