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THE CALIFORNIA QUAIL IN HAWAII

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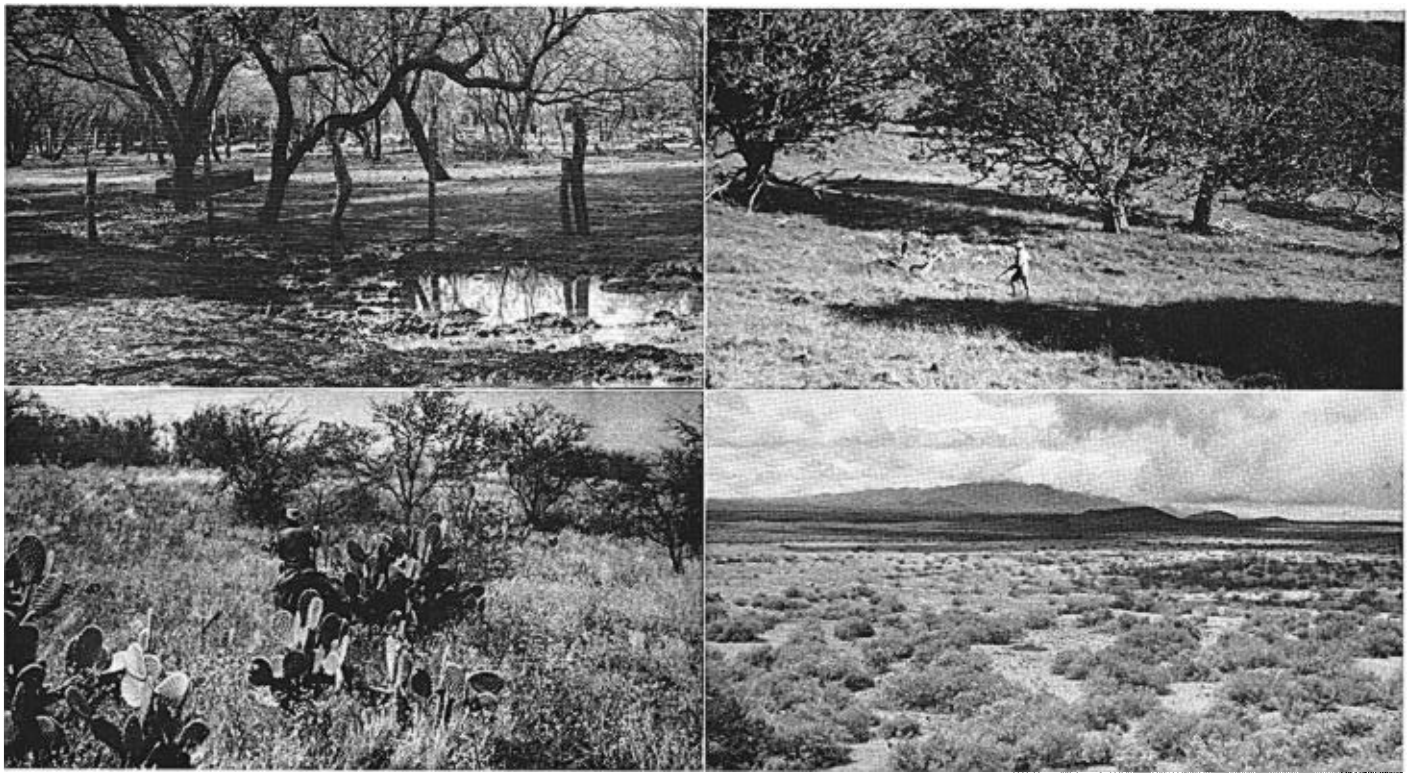
INTRODUCTION

THE study of the California Quail, *Lophortyx californica*, reported here was part of a survey undertaken to determine the distribution and abundance of the various species of game birds on the major Hawaiian Islands and the important factors upon which their welfare depends. This project was the initial step in the Federal Aid-Wildlife Program (1-R) of the Board of Commissioners of Agriculture and Forestry of the Territory of Hawaii. The study was carried on from February, 1946, through July, 1947. Field work was undertaken on all major islands with the exception of Kahoolawe and Niihau. Kahoolawe, a bombing range, was under jurisdiction of the military government. Observations reported for privately-owned Niihau were made by Dr. Harvey I. Fisher.

ACKNOWLEDGMENTS

Assistance was furnished by many individuals but unfortunately, because of limited space, we can acknowledge and thank only a few here. Mr. Colin G. Lennox, President, and Mr. Vernon E. Brock, Director, Division of Fish and Game, and many other employees of the Board of Commissioners of Agriculture and Forestry of the Territory of Hawaii, rendered valuable aid. The owners and operators of ranches and sugar cane and pineapple plantations were likewise helpful in many ways.

Dr. A. Starker Leopold, Museum of Vertebrate Zoology, University of California, identified the specimens of *Lophortyx* collected. Mr. E. Y. Hosaka, University of Hawaii and Bernice P. Bishop Museum, Mr. C. E. Pemberton, Hawaiian Sugar Planters' Association Experiment Station, Drs. E. W. Baker and E. W. Stafford of the United States Department of Agriculture, Dr. Harold St. John, University



(*Upper left*) West of Kaunakakai, Molokai. Vegetation zone A at sea level, *Prosopis chilensis*. Sept. 6, 1946. (*Lower left*) Above Kawaihae, Hawaii. Vegetation zone B, elevation 1,500 feet. April 9, 1946. (*Upper right*) Above Umikoa, Hawaii. Vegetation zone D_3, elevation 5,700 feet, *Acacia Koa* forest, May 10, 1946. (*Lower right*) Near Pohakuloa, Hawaii. Vegetation Zone E_1 grading into E_2, elevation 6,000 feet, *Sophora chrysophylla* and *Myoporum sandwicense*, May 3, 1946.

of Hawaii, and Mr. Gunnar O. Fagerlund, Hawaii National Park, identified some of the plant and animal material referred to in the text. Mr. Paul H. Baldwin, formerly of Hawaii National Park, graciously donated the crops of 15 California Quail he had collected in vegetation zone E_1, and Dr. Robert W. Hiatt, University of Hawaii, contributed the crops of four quail. Dr. Harvey I. Fisher, formerly of the University of Hawaii and now with the University of Illinois, read this manuscript critically and contributed his unpublished observations on the California Quail on Niihau and sight records of quail on Oahu.

GEOGRAPHIC DISTRIBUTION

Although many game species have been introduced into the Hawaiian Islands, the California Quail is one of the few to have become successfully established. This species was brought to Oahu prior to 1855 and was later liberated on all major islands (Caum, 1933). Some of these early plantings became established and by 1890, according to Munro (1944), the California Quail was "very common" on Hawaii in the open forest at 5,000 feet elevation as well as in "very large flocks" in the *Prosopis chilensis* forest on the coast of Molokai; a "very small" importation to Lanai did not succeed. Long-time residents state that populations and ranges of quail on Kauai and Hawaii underwent considerable reduction from 1895 to 1928. These changes were accompanied by increased grazing pressure on both islands and by the development of large areas on Kauai for sugar cane and pineapple.

Until 1940, there were sporadic importations onto the various islands both from California and the game farm on Oahu operated by the Territorial Board of Commissioners of Agriculture and Forestry. In 1933, Caum reported quail "quite common" on Hawaii, "rather common" on Molokai, "less common to very rare" on Oahu, Maui, and Kauai, and without successful liberation on Lanai. Munro (1944) saw "a number on Kauai in 1936 and on Niihau in 1939." This species is well established on Niihau at present (Fisher, MS, 1947). According to Mr. Dexter Fraser, Plantation Manager, Lanai Division of Hawaiian Pineapple Company, 12 pairs of California Quail were liberated on Lanai in 1937–1938. This release is probably responsible for the small population we found on this island. We found no evidence of the California Quail on Oahu, but Harvey I. Fisher (MS) reported seeing singles on three occasions near Kailua in 1945.

Map 1 shows the distribution and densities of the California Quail

in Hawaii, as mapped and censused during 1946 and 1947. The distribution of quail on Niihau was furnished by Fisher (MS), but we have arbitrarily assigned density classes to this island based upon a comparison of his observations on the population status (see p. 10) and our census work on other islands; no total population estimate was computed for Niihau.

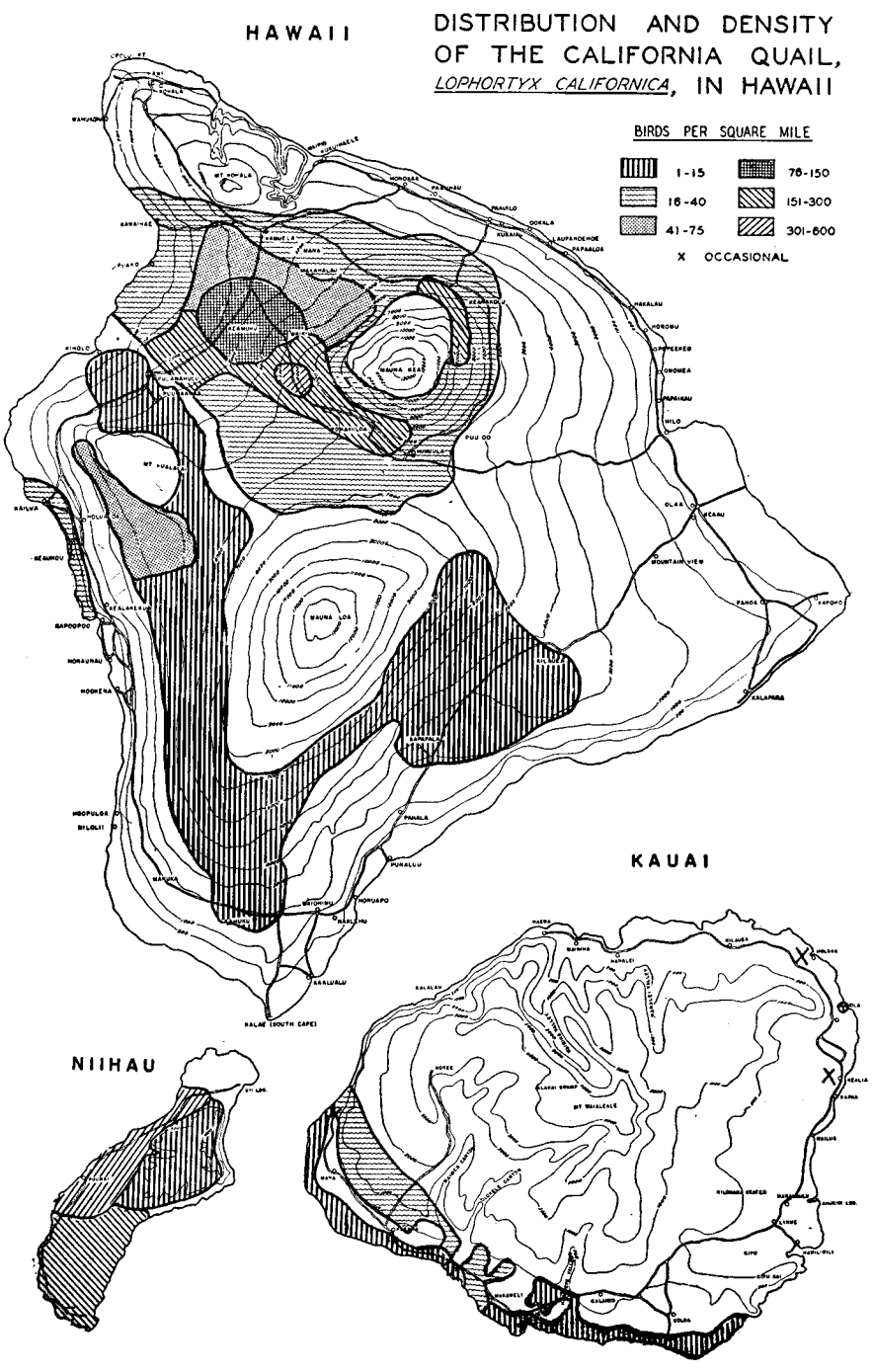
On the island of Hawaii, only the valley form of the California Quail, *L. c. californica* (Shaw and Nodder), was found. The coastal form of the California Quail, *L. c. brunnescens* Ridgway, was the sole race collected on Molokai although formerly *californica* existed here, as evidenced by four skins taken in 1910 and now in the Museum of Vertebrate Zoology at the University of California. On Maui and Kauai, birds resembling both races and their intergrades were found in the same coveys. Similar findings are reported for Niihau (Fisher, MS, 1947). The race occurring on Lanai and Oahu, and which possibly occurs on Kahoolawe, is unknown because no birds were collected by us on these islands.

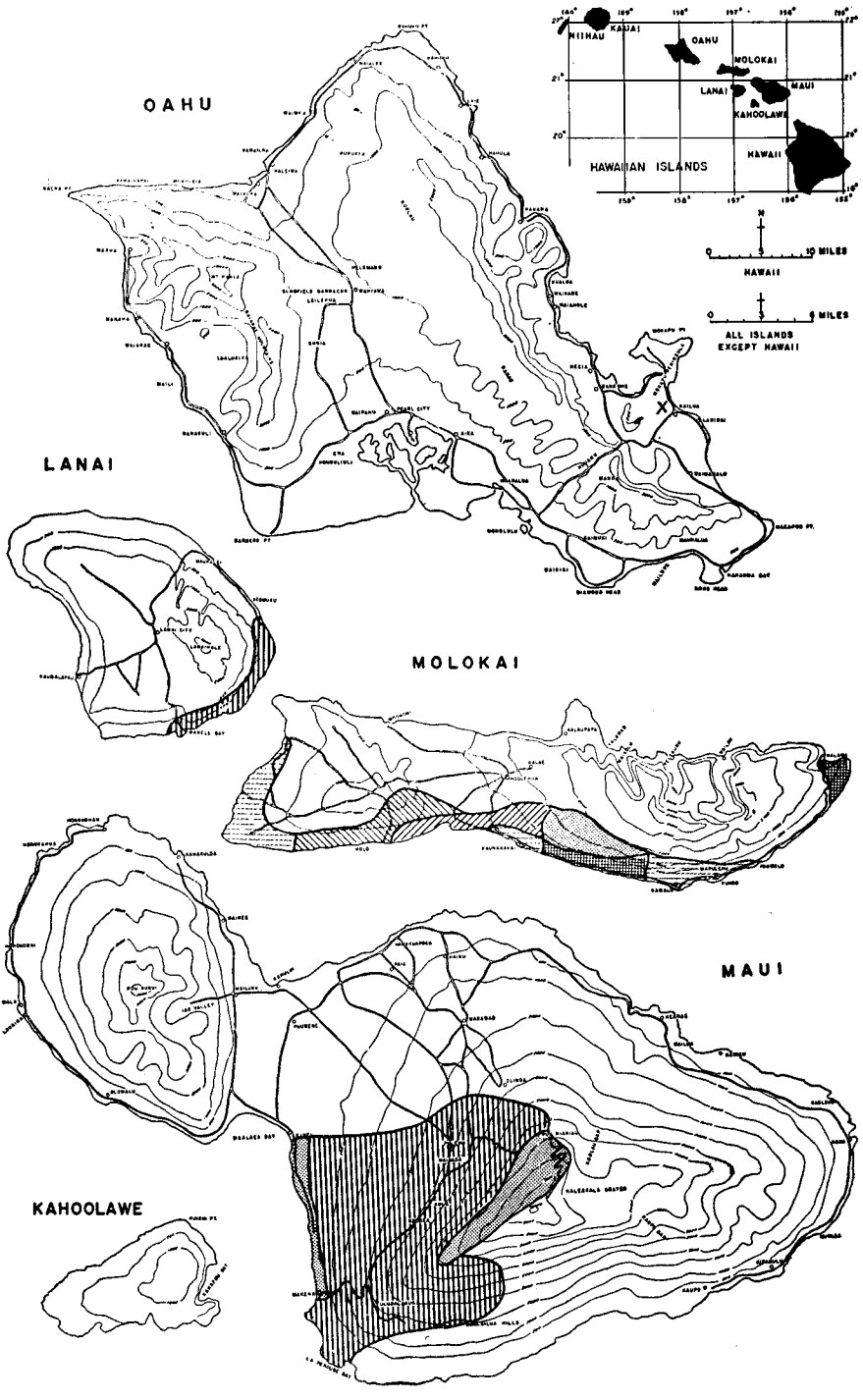
The presence of the two races in Hawaii indicates that some of the original shipments probably came from the inland valleys or the south of California or from Lower California, the native range of the valley race, while others came from the central or northern coast of California, the range of the coastal subspecies. While the ranges of both races in California coincide in places, they are generally restricted to separate localities. However, where introductions for restocking have altered the original distribution in California, racial intermixing has resulted (Grinnell and Miller, 1944). Humidity conditions represent the essential difference between these native ranges, and the races are inferred to be variously adapted to this humidity (Grinnell, Bryant, and Storer, 1918; Sumner, 1935; Grinnell and Miller, 1944). In Hawaii, both races occur under the same climatic conditions and as yet show no apparent differential adaptation to particular environmental factors, including humidity.

The range of the California Quail in Hawaii includes elevations from sea level to 11,000 feet, encompassing a wide variety of environmental conditions. The common use of coastal flats, canyons and deep gullies, mountain slopes and high plateaus, cinder cones, and very rough lava, indicates that such topographic differences are not important limiting factors.

At sea level on the leeward sides of the islands, which embraces the hottest portion of the range, the mean annual air temperature is about 75° F. with the maximum often exceeding 90° F. (Ripperton and Hosaka, 1942). Quail also occur throughout regions with intermediate

MAP I


HAWAII
DISTRIBUTION AND DENSITY OF THE CALIFORNIA QUAIL, LOPHORTYX CALIFORNICA, IN HAWAII
BIRDS PER SQUARE MILE
1-15
16-40
41-75
76-150
151-300
301-600
X OCCASIONAL
MAUNA KEA
MAUNA LOA
PUU OO
HILO
KAILUA
KEALAKEKUA
NAALEHU
KALAE (SOUTH CAPE)
KAUAI
NIIHAU


OAHU
LANAI
MOLOKAI
MAUI
KAHOOLAWE
NIIHAU
KAUAI
OAHU
MOLOKAI
LANAI
MAUI
KAHOOLAWE
HAWAII
HAWAIIAN ISLANDS
N
0 10 MILES
HAWAII
0 6 MILES
ALL ISLANDS EXCEPT HAWAII

temperatures to areas on or near mountain peaks where the mean annual air temperature may be 40° F. The lowest temperature recorded in the range of quail is 25° F. at 6,685 feet on Hawaii (Feldwisch, 1941). During the winter, quail living at extremely high elevations descend to the lower limits of the snow line which occasionally reaches down to 10,000 feet elevation.

The present range is restricted primarily to the leeward sides of the islands and generally includes variations in rainfall from less than 20 to 60 inches annually. However, in a few places, portions of the range may receive a precipitation of 80 or 100 inches annually (Rainfall maps prepared by U. S. Weather Bureau, Honolulu). In these areas of high precipitation the climate is moist and cool, commonly having mist of two to three or more days' duration. Above approximately 5,000 feet elevation, the range extends around the volcanic peaks of Haleakala on Maui and Mauna Kea on Hawaii to the windward sides, but here it is above the belt of maximum precipitation which may exceed 450 inches annually, and rainfall conditions approximate those found in places in the leeward range. While variations in annual rainfall are important throughout quail range, differences in monthly precipitation may be even more significant ecologically. Monthly rainfall throughout the Hawaiian Islands often varies extremely from year to year so that one month may have the highest precipitation in one year and the lowest in another.

California Quail occur in certain habitat conditions on land which is used for grazing or without present economic use. The extensiveness and intensiveness of grazing and amount of available water, either as rainfall, dew, succulence, or sources provided for livestock, are of utmost importance and directly influence the presence and density of the populations. There is no suitable range in areas cultivated for sugar cane or pineapple because they lack an interspersion of desirable food and cover plants, but limited populations may be found occasionally in homestead areas with small truck gardens. Dense rain forests likewise preclude quail because of their extensive and dense cover, heavy rainfall, and lack of suitable food. Where the land-use pattern permits, populations of quail are highest on the most fertile soils within the range.

POPULATIONS

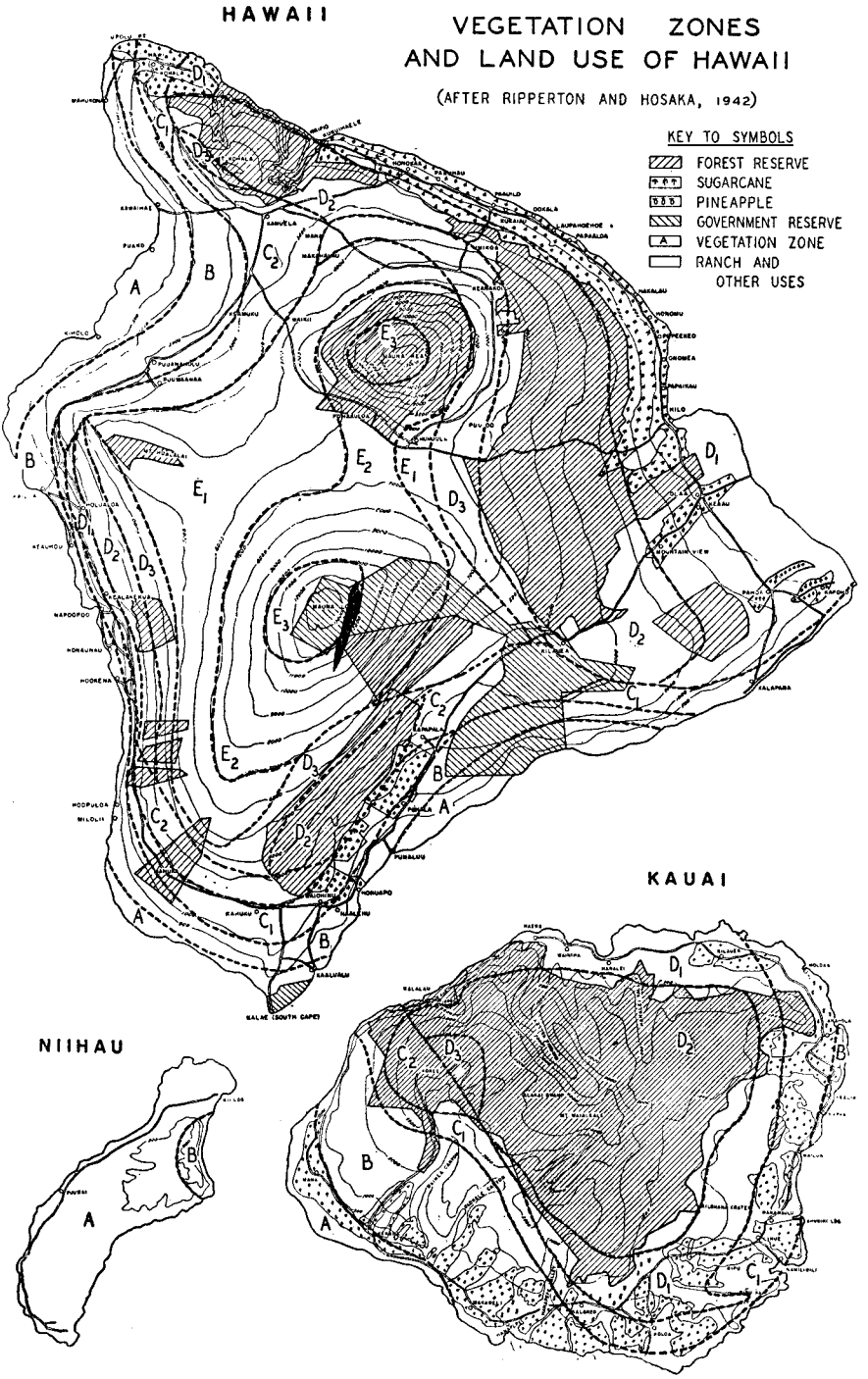
The distribution of the California Quail in Hawaii is given in Table 1, and total populations and frequency of density classes are listed in Table 2 as mapped and censused in 1946 and 1947. A total of 1,803 square miles was occupied by 77,650 California Quail with densities

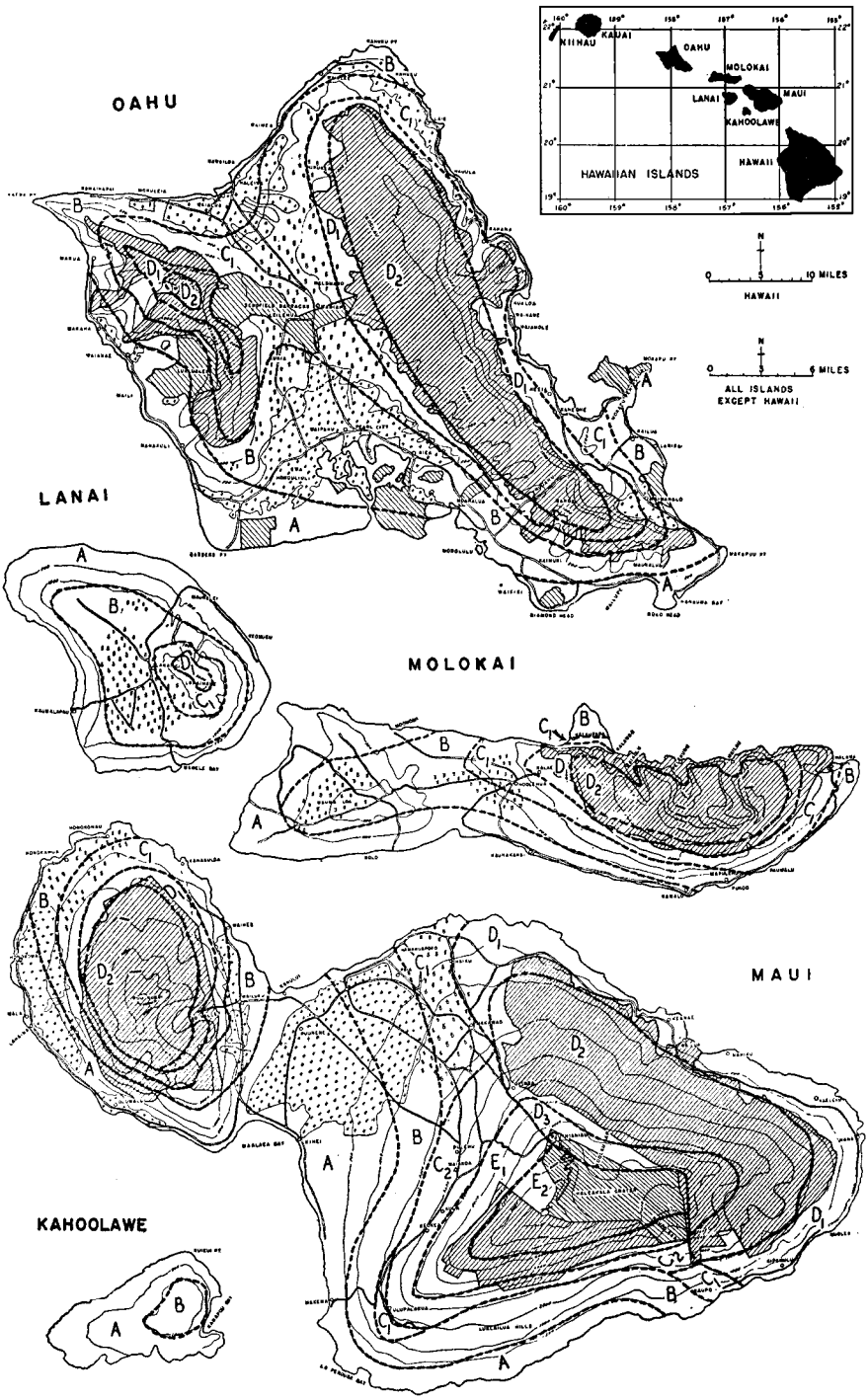
TABLE 1

DISTRIBUTION BY VEGETATION ZONE OF CALIFORNIA QUAIL RANGE IN HAWAII

	Hawaii	*Kauai*	*Lanai*	*Maui*	*Molokai*	*Total*
Vegetation Zone A						
Square miles	249	23	72	121	64	529
Square miles occupied	76	11	9	32	43	171
Per cent zone occupied	31	48	13	26	67	32
Per cent total range						.9
Vegetation Zone B						
Square miles	408	116	57	138	74	793
Square miles occupied	178	41	0	25	23	267
Per cent zone occupied	44	35	0	18	31	34
Per cent total range						.15
Vegetation Zone C_1						
Square miles	194	88	10	54	46	392
Square miles occupied	21	0	0	2	6	29
Per cent zone occupied	11	0	0	4	13	7
Per cent total range						.2
Vegetation Zone C_2						
Square miles	316	11	0	61	0	388
Square miles occupied	257	0	0	37	0	294
Per cent zone occupied	81	0	0	61	0	76
Per cent total range						.16
Vegetation Zone D_1						
Square miles	464	113	2	97	32	708
Square miles occupied	0	0	0	0	0	0
Per cent zone occupied	0	0	0	0	0	0
Per cent total range						.0
Vegetation Zone D_2						
Square miles	790	194	0	151	44	1,179
Square miles occupied	14	0	0	0	0	14
Per cent zone occupied	2	0	0	0	0	1
Per cent total range						.1
Vegetation Zone D_3						
Square miles	353	10	0	23	0	386
Square miles occupied	298	0	0	4	0	302
Per cent zone occupied	84	0	0	17	0	78
Per cent total range						.17
Vegetation Zone E_1						
Square miles	647	0	0	39	0	686
Square miles occupied	553	0	0	32	0	585
Per cent zone occupied	85	0	0	82	0	85
Per cent total range						.32
Vegetation Zone E_2						
Square miles	503	0	0	44	0	547
Square miles occupied	129	0	0	7	0	136
Per cent zone occupied	26	0	0	16	0	25
Per cent total range						.8
Vegetation Zone E_3						
Square miles	106	0	0	0	0	106
Square miles occupied	5	0	0	0	0	5
Per cent zone occupied	5	0	0	0	0	5
Per cent total range						trace
TOTAL, *Vegetation Zones*						
Square miles	4,030	555	141	728	260	5,714
Square miles occupied	1,531	52	9	139	72	1,803
Per cent island occupied	38	9	6	19	28	32
Per cent total range	85	3	trace	8	4	

MAP 2


HAWAII
VEGETATION ZONES
AND LAND USE OF HAWAII
(AFTER RIPPERTON AND HOSAKA, 1942)
KEY TO SYMBOLS
FOREST RESERVE
SUGARCANE
PINEAPPLE
GOVERNMENT RESERVE
VEGETATION ZONE
RANCH AND OTHER USES
KAUAI
NIIHAU


OAHU
LANAI
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MAUI
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NIIHAU
KAUAI
OAHU
MOLOKAI
LANAI
MAUI
KAHOOLAWE
HAWAII
HAWAIIAN ISLANDS
10 MILES
HAWAII
5 MILES
ALL ISLANDS
EXCEPT HAWAII

varying from less than 15 to 600 birds per square mile. These data are presented by Vegetation Zones following the classification of Ripperton and Hosaka (1942) which offers a convenient means of grouping vegetative types in Hawaii (Map 2 and pp. 29–36). Average densities were not computed because they fail to show the variation or frequency of densities within a given range and are of little value in range evaluation. Densities of quail in Hawaii are comparable to those in California (McLean, 1930; Sumner, 1935; Glading, 1938 and 1941).

A summary of the status of quail on Niihau has been given by Fisher (MS, 1947): "These quail are abundant in the kiawe-covered, *Prosopis chilensis*, lowlands at the base of the mountains and in the canyons. They are concentrated especially about the water sumps, but coveys are widespread. Literally hundreds of these birds were to be found feeding, in groups on the ground, and perched in kiawe trees around the waterholes. In the flatter, more open coastal areas they are not as numerous, but on checking several locations in August it was found that even here one could average seeing more than 100 birds in a half-mile walk. In the grassy, plateau country there were few birds; one could ride for half an hour and see only 10 or 15 birds. Available water in this area is probably the limiting factor."

Our census method consisted of taking sample strip counts throughout the different vegetation zones, directing attention toward minor differences in cover types. Observations were made by one or two, and occasionally three, observers from horseback, automobile, and on foot, depending upon the specific type of cover. This technique is similar to the one used in California (Glading, 1941; Emlen and Glading, 1945). All islands were not censused during the same season because of limitations in time. Population figures for the island of Hawaii represent pre-breeding birds while those for the remaining islands are post-breeding. The ranges of quail on these latter islands are primarily in dry zones, and collections in 1946 showed a low ratio of birds of the year to adults, indicating poor reproduction during the breeding season of that year. Also, large coveys were found during and immediately following this breeding season, indicating a lack of pairing and breeding. Since population estimates are based primarily upon covey formation rather than isolated pairs, we believe these post-breeding figures correspond, with but little reservation, to the pre-breeding figures given for Hawaii.

The best ranges of California Quail occur in vegetation zones A, B, C_2, E_1, and E_2. All these zones have high densities and populations, and medium to high percentages of zonal occupancy. Because of

TABLE 2

POPULATIONS OF THE CALIFORNIA QUAIL BY VEGETATION ZONE

		Distribution of density classes in birds per square mile											
		1–15		16–40		41–75		76–150		151–300		301–600	
	Total population	Miles	Per cent	Miles	Per cent	Miles	Per cent	Miles	Per cent	Miles	Per cent	Miles	Per cent
Vegetation Zone—A													
Hawaii	1,750	10	13	66	87								
Kauai	110	11	100										
Lanai	100	9	100										
Maui	620	25	78			7	22						
Molokai	8,590			16	37			6	14	11	26	10	23
Total	11,170	55	32	82	48	7	4	6	4	11	6	10	6
Per cent total population	14												
Vegetation Zone—B													
Hawaii	8,730	52	29	64	36	24	14	18	10	20	11		
Kauai	700	12	29	29	71								
Lanai	0												
Maui	250	25	100										
Molokai	2,600			6	26	6	26	6	26	2	9	3	13
Total	12,280	89	34	99	37	30	11	24	9	22	8	3	1
Per cent total population	16												
Vegetation Zone—C_1													
Hawaii	340	13	62	8	38								
Kauai	0												
Lanai	0												
Maui	20	2	100										
Molokai	400					5	83	1	17				
Total	760	15	52	8	28	5	17	1	3				
Per cent total population	1												
Vegetation Zone—C_2													
Hawaii	10,220	42	16	147	57	32	13	29	11	7	3		
Kauai	0												
Lanai	0												
Maui	370	37	100										
Molokai	0												
Total	10,590	79	27	147	50	32	11	29	10	7	2		
Per cent total population	14												
Vegetation Zone—D_1	No California quail												
Vegetation Zone—D_2													
Hawaii	350			14	100								
Kauai	0												
Lanai	0												
Maui	0												
Molokai	0												
Total	350			14	100								
Per cent total population	trace												

TABLE 2 (*Continued*)
POPULATIONS OF THE CALIFORNIA QUAIL BY VEGETATION ZONE

		Distribution of density classes in birds per square mile											
		1–15		16–40		41–75		76–150		151–300		301–600	
	Total population	Miles	Per cent	Miles	Per cent	Miles	Per cent	Miles	Per cent	Miles	Per cent	Miles	Per cent
Vegetation Zone—D_3													
Hawaii	5,700	168	56	99	33	31	11						
Kauai	0												
Lanai	0												
Maui	180	2	50			2	50						
Molokai	0												
Total	5,880	170	56	99	33	33	11						
Per cent total population	8												
Vegetation Zone—E_1													
Hawaii	24,890	273	49	177	32	59	11	1	T	32	6	11	2
Kauai	0												
Lanai	0												
Maui	640	27	84			5	16						
Molokai	0												
Total	25,530	300	51	177	30	64	11	1	T	32	6	11	2
Per cent total population	33												
Vegetation Zone—E_2													
Hawaii	10,450	81	63	8	6					39	30	1	1
Kauai	0												
Lanai	0												
Maui	520					7	100						
Molokai	0												
Total	10,970	81	60	8	5	7	5			39	29	1	1
Per cent total population	14												
Vegetation Zone—E_3													
Hawaii	120			5	100								
Kauai	0												
Lanai	0												
Maui	0												
Molokai	0												
Total	120			5	100								
Per cent total population	trace												

			Distribution of density classes in birds per square mile											
			1–15		16–40		41–75		76–150		151–300		301–600	
	Total population	*Per cent Total Pop.*	Miles	Per cent	Miles	Per cent	Miles	Per cent	Miles	Per cent	Miles	Per cent	Miles	Per cent
Vegetation Zones—TOTAL														
Hawaii	62,550	81	639	42	588	38	146	10	48	3	98	6	12	1
Kauai	810	1	23	44	29	56								
Lanai	100	trace	9	100										
Maui	2,600	3	118	85			21	15						
Molokai	11,590	15			22	31	11	15	13	18	13	18	13	18
Total	77,650		789	44	639	36	178	10	61	3	111	6	25	1

predominantly low densities, zone D_3 is evaluated as range of intermediate quality, although it possesses a large amount of occupied area and a medium population. Zones C_1, D_2, and E_3 are considered poor range for quail as indicated by low densities, populations, and percentages of zonal occupancy. No California Quail occur in zone D_1.

FOODS

Most plants in Hawaii bear fruit, seeds, and foliage the year around, although there may be periods of more abundant production by individual species. Vegetation is retarded by low temperatures during

TABLE 3

FOODS OF THE CALIFORNIA QUAIL IN VEGETATION ZONE *A*

Species	*Occurrence in range*[1]	*Food class*	*Per cent crop volume*	*Number occurrences in crops*	*Number occurrences in gizzards*
PLANTS					
Prosopis chilensis	abundant	1	62.7	31	31
Leucaena glauca	common	1	30.1	25	10
Portulaca oleracea	rare	2	2.1	3	2
Waltheria americana	occasional	2	2.0	16	21
Sida rhombifolia	very rare	3	0.6	1	0
Setaria verticillata	common	3	0.5	10	10
Abutilon molle	rare	3	0.1	4	8
Sida cordifolia and Sida fallax[2]	occasional & common	3	0.1	5	7
Atriplex semibaccata	common	3	T	1	0
Chenopodium ambrosioides	very rare	3	T	1	0
Chloris inflata	abundant	3	T	2	0
Cyperus polystachos	very rare	3	T	2	0
Dodonaea viscosa	very rare	3	T	1	1
Malvastrum coromandelianum	occasional	3	T	1	13
Opuntia megacantha	occasional	3	T	1	1
Oxalis corniculata	very rare	3	T	1	0
Unidentified seeds			T	3	3
Cassia Leschenaultiana	very rare			0	1
TOTAL			98.2		
ANIMALS					
Blapstinus dilitatus		2	1.8	3	1
Bruchus sallaei		3	T	1	0
Coleoptera (unid.)		3	T	1	2
Carpophilus humeralis		3	T	1	0
Camponotus variegatus hawaiiensis		3	T	2	0
TOTAL			1.8		

Total crops, 31
Crops with measurable volumes, 31
Total gizzards, 31

[1] Based upon Ripperton and Hosaka (1942) and our field work.
[2] Seeds of these species are impossible to distinguish and are combined here.

winter at very high altitudes, while growth and seed production are delayed by periods of drouth in other regions, particularly the leeward coastal areas. However, these variations are not of sufficient magnitude to warrant segregation of this food analysis into definite seasons. Plants vary by species and abundance according to the various climatic, soil, and other physiographic conditions of Hawaii. In order to evaluate the importance of plants in the dietary of the California Quail, we again followed the classification of Vegetation Zones of Hawaii which correlates the essential features of the environment on all islands.

Foods of grown birds.—The crops and gizzards of 145 California Quail were collected and analyzed in the field. Although limiting the size of the sample, an analysis of foods made simultaneously with field work provided essential information required in on-the-spot range analysis. Contents of crops and gizzards were dried and food items separated and identified. Each type of food was measured volumetrically in cubic centimeters and totalled for respective vegetation zones by aggregate volume (Martin, Gensch, and Brown, 1946). In order to establish a useful tool for range evaluation, food items were arbitrarily assigned to three classes (class 1, 2, and 3) based upon their respective volumes in crops by vegetation zone. Frequency of occurrence was listed separately for crops and gizzards. When a given food occurred in more than half of the crops of a vegetation zone, its frequency of occurrence was considered "high," and when a food occurred in less than half of the sample, its frequency of occurrence in crops was judged "low."

Foods of the California Quail in Hawaii are given by vegetation zone in Tables 3 through 9. A total of 93 foods was found, of which 67 were plant species and 26 animal items. Although the sample is small in some vegetation zones, volume and frequency distributions follow a uniform pattern and we have assigned class values to all foods on a uniform basis.

Class 1 foods consist of 11 plant species which occurred in volumes of 11 per cent and over. Class 2 foods include 26 plant species (seven of which are also class 1 in some zone) and four animals found in crop volumes from one to 11 per cent. Foods in these two classes are considered important because of their volumes in the dietary. Where they are common in the range, their frequency of occurrence in crops is usually high and they form staple foods. Plants which are uncommon in the range customarily show low frequencies of occurrence, but their volumes indicate they are probably sought.

TABLE 4

FOODS OF THE CALIFORNIA QUAIL IN VEGETATION ZONE B

Species	*Occurrence in range*	*Food class*	*Per cent crop volume*	*Number occurrences in crops*	*Number occurrences in gizzards*
PLANTS					
Cassia Leschenaultiana	common	1	66.3	5	5
Diospyros ferrea	very rare	2	8.4	1	0
Waltheria americana	common	2	4.4	7	9
Sida rhombifolia	occasional	2	4.2	1	1
Leucaena glauca	abundant	2	2.8	3	1
Desmodium uncinatum	rare	2	2.1	1	0
Opuntia megacantha	common	2	2.1	1	3
Galinsoga parviflora	occasional	2	1.3	3	2
Atriplex semibaccata	rare	2	1.3	1	1
Hypochaeris radicata	very rare	2	1.1	1	0
Prosopis chilensis	common	2	1.1	2	3
Dodonaea viscosa	occasional	2	1.1	3	6
Portulaca cyanosperma	very rare	3	0.8	2	0
Solanum nodiflorum	occasional	3	0.6	1	1
Abutilon molle	occasional	3	0.6	3	6
Medicago hispida	occasional	3	0.4	2	4
Trifolium repens	very rare	3	0.4	1	2
Bidens pilosa	common	3	0.2	2	0
Indigofera suffruticosa	rare	3	0.2	3	1
Oxalis corniculata	rare	3	0.2	2	3
Sida cordifolia and Sida fallax	common & abundant	3	0.2	2	5
Unidentified plant material			0.2	2	1
Digitaria violascens	occasional	3	T	1	1
Euphorbia hirta	occasional	3	T	1	1
Medicago lupulina	very rare	3	T	2	2
Melilotus indica	occasional	3	T	1	1
Tephrosia purpurea	rare	3	T	1	0
Setaria verticillata	occasional	3	T	1	0
Unidentified seeds			T	1	2
Bromus catharticus	very rare			0	1
Desmodium tortuosum	rare			0	1
Malva parviflora	occasional			0	1
Nicandra Physalodes	very rare			0	1
TOTAL			100.0		
ANIMALS					
Blapstinus dilitatus		3	T	1	1
Camponotus variegatus hawaiiensis		3	T	1	0
Hemiptera (unid.)		3	T	1	0
Arachnida (unid.)		3	T	1	0
TOTAL			trace		

Total crops, 12
Crops with measurable volumes, 12
Total gizzards, 12

The remaining 37 plants and 22 animals were assigned to class 3. All occurred as less than one per cent of the crop volume and showed low frequencies of occurrence in crops. These are of less importance

TABLE 5

FOODS OF THE CALIFORNIA QUAIL IN VEGETATION ZONE C_2

Species	*Occurrence in range*	*Food class*	*Per cent crop volume*	*Number occurrences in crops*	*Number occurrences in gizzards*
PLANTS					
Hypochaeris radicata	common	1	33.5	6	0
Medicago lupulina	common	1	31.1	6	7
Sonchus oleraceus	very rare	1	11.4	2	1
Urtica sp.	very rare	2	6.9	1	1
Cirsium vulgare	common	2	5.7	8	5
Bromus catharticus	common	2	4.5	4	2
Trifolium repens	occasional	2	3.9	2	2
Medicago hispida	occasional	2	1.9	6	5
Oxalis corniculata	very rare	3	0.1	4	3
Sporobolus capensis	common	3	0.1	3	1
Euphorbia hirta	very rare	3	T	2	6
Verbena litoralis	common	3	T	1	0
Vicia sativa	occasional	3	T	1	3
Unidentified seeds			T	2	3
Malva parviflora	occasional			0	1
Paspalum sp.				0	1
TOTAL			99.1		
ANIMALS					
Blapstinus dilitatus		3	0.7	2	1
Hemiptera (unid.)		3	0.1	1	0
Nysius coenosulus		3	0.1	4	0
Agrotis ypsilon		3	T	1	0
Conoderus exsul		3	T	2	0
Coleoptera (unid.)		3	T	0	1
TOTAL			0.9		

Total crops, 9
Crops with measurable volumes, 8
Crops empty, 1
Total gizzards, 9

than foods in the other classes. Where plants of this class are common in the range, they must be non-preferred and, where uncommon, are represented rarely in the dietary due to their general unavailability. Certain plants, although occurring in small amounts in the diet, may be essential to the bird's welfare either individually or in the aggregate, but this importance escapes detection because such a classification fails to evaluate fairly food species occurring in small amounts.

Swezey (1937) reported the food of nine California Quail taken at Kanoa, Molokai in 1928. These included seeds and pod fragments of *Acacia farnesiana*, seeds and pod fragments of *Prosopis chilensis*, seeds of *Chaetochloa verticillata* (since called *Setaria verticillata*), seeds of *Chenopodiaceae*, one "Amaranth" seed, six "other seeds," one larva of *Diremptus epitragus*, one adult *Bruchus sallaei*, and one pupa

(unidentified). In general, these findings agree with ours for this area of Molokai. However, we found no birds eating *Acacia farnesiana*,

TABLE 6

FOODS OF THE CALIFORNIA QUAIL IN VEGETATION ZONE D_3

Species	*Occurrence in range*	*Food class*	*Per cent crop volume*	*Number occurrences in crops*	*Number occurrences in gizzards*
PLANTS					
Trifolium repens	occasional	1	81.0	9	9
Hypochaeris radicata	common	2	9.3	9	2
Stellaria media	very rare	2	7.1	6	2
Sporobolus capensis	occasional	2	1.2	6	6
Silene gallica	very rare	3	0.1	1	0
Cynodon Dactylon	very rare	3	T	1	1
Euphorbia hirta	very rare	3	T	1	0
Modiola caroliniana	occasional	3	T	3	3
Oxalis corniculata	very rare	3	T	2	1
Rumex acetosella	common	3	T	3	5
Verbena litoralis	very rare	3	T	1	0
Geranium carolinianum var. *australe*	occasional			0	2
Plantago sp.				0	1
Rubus hawaiensis	common			0	3
Unidentified seeds				0	3
TOTAL			98.7		
ANIMALS					
Lepidoptera (unid.)		2	1.0	1	0
Nysius coenosulus		3	0.2	1	0
Oechalia pacifica		3	0.1	1	0
Agrotis ypsilon		3	T	1	0
Blapstinus dilitatus		3	T	1	0
Coleoptera (unid.)		3	T	1	0
Nesomicromus vagus		3	T	1	0
TOTAL			1.3		

Total crops, 10
Crops with measurable volumes, 10
Total gizzards, 10

but it occurs commonly in the lower leeward vegetation zones occupied by quail.

Of the large variety of foods eaten in Hawaii, only 13 are also taken by California Quail in California (Sumner, 1935; Glading, Biswell, and Smith, 1940; Emlen and Glading, 1945). Three of these (*Cirsium sp.*, *Stellaria media*, and *Trifolium sp.*) are among our class 1 foods, four (*Atriplex sp.*, *Bromus sp.*, *Medicago hispida*, and *Rumex acetosella*) are class 2 foods, and the rest (*Amaranthus sp.*, *Anagallis arvensis*, *Erodium cicutarium*, *Lolium multiflorum*, *Rubus spp.*, and *Silene gallica*) belong to class 3. This difference in diet reflects variations in the plant

cover in these widely-separated lands and emphasizes the ability of this bird to utilize new foods in its adopted range.

TABLE 7

FOODS OF THE CALIFORNIA QUAIL IN VEGETATION ZONE E_1

Species	*Occurrence in range*	*Food class*	*Per cent crop volume*	*Number occurrences in crops*	*Number occurrences in gizzards*
PLANTS					
Hypochaeris radicata	common	1	27.3	26	16
Lepidium auriculatum	very rare	1	20.7	10	7
Cirsium vulgare	occasional	1	12.8	12	12
Trifolium repens	occasional	2	8.7	6	5
Medicago lupulina	occasional	2	7.9	21	23
Carex wahuensis	very rare	2	3.5	5	3
Bromus catharticus	common	2	2.9	11	9
Eupatorium adenophorum	abundant	2	2.1	3	0
Anagallis arvensis	occasional	3	0.8	3	0
Lolium multiflorum	occasional	3	0.6	1	1
Sonchus oleraceus	very rare	3	0.5	4	1
Solanum nodiflorum	very rare	3	0.4	3	3
Melilotus indica	very rare	3	0.4	1	1
Anthoxanthum odoratum	occasional	3	0.3	2	0
Malva parviflora	very rare	3	0.2	4	8
Rumex acetosella	common	3	0.2	4	4
Stellaria media	very rare	3	0.2	3	1
Medicago hispida	occasional	3	0.1	1	0
Amaranthus viridis	very rare	3	T	2	2
Digitaria violascens	occasional	3	T	1	1
Dodonaea viscosa	occasional	3	T	9	18
Erodium cicutarium	occasional	3	T	2	0
Geranium carolinianum var. *astrale*	rare	3	T	2	3
Oxalis corniculata	very rare	3	T	2	0
Panicum tenuifolium	common	3	T	2	0
Sophora chrysophylla	common	3	T	3	3
Sporobolus capensis	occasional	3	T	5	0
Styphelia Tameiameiae	occasional	3	T	1	2
Urtica sp.	very rare	3	T	1	0
Unidentified plant material			T	9	5
Unidentified seeds			T	6	6
Abutilon molle	very rare			0	1
Chenopodium oahuense	occasional			0	1
Chenopodium ambrosioides	rare			0	1
Myoporum sandwicense	common			0	1
Vicia sativa	rare			0	3
TOTAL			89.6		
ANIMALS					
Agrotis ypsilon		2	7.4	7	1
Cirphis unipuncta		2	2.2	4	0
Sarcophagidae (unid.)		3	0.6	1	0
Nysius coenosulus		3	0.2	6	0
Insecta (unid.)		3	T	5	0
Blapstinus dilitatus		3	T	1	0
Curculionidae (unid.)		3	T	1	0
Coleoptera (unid.)		3	T	1	0
Dermaptera (unid.)		3	T	1	0

TABLE 7—*Continued*

Species	*Occurrence in range*	*Food class*	*Per cent crop volume*	*Number occurrences in crops*	*Number occurrences in gizzards*
PLANTS					
Elateridae (unid.)		3	T	1	0
Hemiptera (unid.)		3	T	4	0
Lepidoptera (unid.)		3	T	4	0
Lumbricus sp.		3	T	2	0
Limacidae (unid.)		3	T	2	0
Miridae (unid.)		3	T	2	0
Pantomorus godmani		3	T	1	0
TOTAL			10.4		

Total crops, 47
Crops with measurable volume, 33
Crops with traces, 13[1]
Crops empty, 1
Total gizzards, 46

[1] Twelve of these were not analyzed volumetrically, hence are included here by occurrence only.

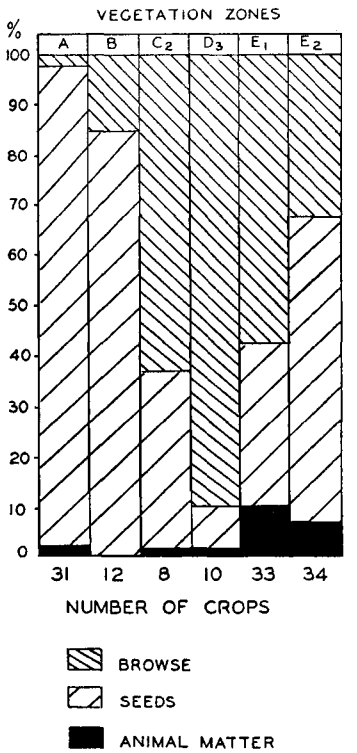

FIGURE 1.—Foods of the California Quail classified as browse, seeds, and animal matter, by vegetation zone.

Figure 1 presents the foods by vegetation zone and classified according to relative amounts of animal matter, seeds, and browse. In general, animal matter ranks lowest, varying from a trace in zone B to 10 per cent in zone E_1. Adult, larval, and nymphal stages of various insects which are harmful, neutral, and beneficial to agriculture constituted most of the animal food. Traces of *Lumbricus*, limacidae, and arachnida comprised the remainder.

In California, animal matter varied from 0.3 per cent to 3.0 per cent of the annual dietary of California Quail (Grinnell, Bryant, and Storer,

TABLE 8

FOODS OF THE CALIFORNIA QUAIL IN VEGETATION ZONE E_2

Species	*Occurrence in range*	*Food class*	*Per cent crop volume*	*Number occurrences in crops*	*Number occurrences in gizzards*
PLANTS					
Lepidium auriculatum	very rare	1	24.4	19	13
Verbena litoralis	very rare	1	14.8	16	13
Stellaria media	rare	1	11.4	3	4
Argemone alba var. *glauca*	very rare	2	8.9	4	0
Hypochaeris radicata	very rare	2	7.0	5	3
Sonchus oleraceus	very rare	2	5.8	4	0
Sida rhombifolia	very rare	2	4.5	6	6
Sophora chrysophylla	abundant	2	4.1	11	12
Anthoxanthum odoratum	rare	2	3.2	1	0
Rumex acetosella	rare	2	3.2	1	2
Bromus catharticus	very rare	2	2.0	11	1
Unidentified plant material			1.6	3	1
Oxalis corniculata	very rare	3	0.9	3	2
Chenopodium ambrosioides	very rare	3	0.5	2	1
Trifolium repens	very rare	3	0.4	2	0
Amaranthus viridis	very rare	3	0.3	5	2
Malva parviflora	very rare	3	0.3	4	1
Medicago lupulina	very rare	3	0.1	2	0
Chenopodium oahuense	very rare	3	T	1	1
Panicum tenuifolium	occasional	3	T	5	0
Eragrostis grandis	very rare	3	T	1	0
Cynodon Dactylon	very rare	3	T	1	0
TOTAL			93.4		
ANIMALS					
Agrotis ypsilon		2	5.4	6	0
Nysius coenosulus		3	0.9	3	0
Lepidoptera (unid.)		3	0.3	2	0
Diplazon laetatorius		3	T	2	0
Tenebrionidae (unid.)		3	T	1	1
Hymenoptera (unid.)		3	T	1	0
Coeloptera (unid.)				0	1
TOTAL			6.6		

Total crops, 36
Crops with measurable volumes, 34
Crops with traces, 2
Total gizzards, 24

TABLE 9

FOODS, BY FOOD CLASS, OF THE CALIFORNIA QUAIL IN ALL VEGETATION ZONES

Species and parts eaten[1]	*Food class by vegetation zone*					
	A	*B*	C_2	D_3	E_1	E_2
PLANTS						
Abutilon molle, seed	3	3			G	
Amaranthus viridis, seed					3	3
Anagallis arvensis, seed and pod					3	
Anthoxanthum odoratum, seed					3	2
Argemone alba var. *glauca*, seed						2
Atriplex semibaccata, seed; leaf T	3	2				
Bidens pilosa, seed		3				
Bromus catharticus, seed		G	2		2	2
Carex wahuensis, seed					2	
Cassia Leschenaultiana, seed ¾; blossom ¼	G	1				
Chenopodium oahuense, seed					G	3
Chenopodium ambrosioides, seed	3				G	3
Chloris inflata, seed	3					
Cirsium vulgare, seed			2		1	
Cynodon Dactylon, seed				3		3
Cyperus polystachos, seed	3					
Desmodium tortuosum, seed and pod		G				
Desmodium uncinatum, seed and pod		2				
Digitaria violascens, seed		3			3	
Diospyros ferrea, fruit		2				
Dodonaea viscosa, seed	3	2			3	
Eragrostis grandis, seed						3
Erodium cicutarium, seed					3	
Eupatorium adenophorum, bud					2	
Euphorbia hirta, seed		3	3	3		
Galinsoga parviflora, flower; seed T		2				
Geranium carolinianum var. *australe*, seed				G	3	
Hypochaeris radicata, flower, stem, leaf; seed T		2	1	2	1	2
Indigofera suffruticosa, seed		3				
Lepidium auriculatum, seed ½; leaf, flower ½					1	1
Leucaena glauca, seed	1	2				
Lolium multiflorum, seed					3	
Malva parviflora, seed		G	G		3	3
Malvastrum coromandelianum, seed	3					
Medicago hispida, leaf; seed T		3	2		3	
Medicago lupulina, seed ½; leaf, flower ½		3	1		2	3
Melilotus indica, seed ½; leaf ½		3			3	
Modiola caroliniana, seed				3		
Myoporum sandwicense, seed					G	
Nicandra Physalodes, seed		G				
Opuntia megacantha, fruit; seed T	3	2				
Oxalis corniculata, seed	3	3	3	3	3	3
Panicum tenuifolium, seed					3	3
Paspalum sp., seed			G			
Plantago sp., seed				G		
Portulaca cyanosperma, leaf		3				
Portulaca oleracea, seed and pod ¾; leaf ¼	2					
Prosopis chilensis, seed, pod; leaf T	1	2				
Rubus hawaiensis, seed				G		
Rumex acetosella, leaf; seed T				3	3	2
Setaria verticillata, seed	3	3				
Sida cordifolia and *Sida fallax*, seed; leaf T	3	3				
Sida rhombifolia, seed; leaf, blossom T	3	2				2
Silene gallica, seed				3		

TABLE 9 (*Continued*)

FOODS, BY FOOD CLASS, OF THE CALIFORNIA QUAIL IN ALL VEGETATION ZONES

Species and parts eaten[1]	*Food class by vegetation zone*					
	A	*B*	C_2	D_3	E_1	E_2
Solanum nodiflorum, seed and fruit		3			3	
Sonchus oleraceus, flower; leaf T			1		3	2
Sophora chrysophylla, seed ½; blossom ½					3	2
Sporobolus capensis, seed; leaf T			3	2	3	1
Stellaria media, seed, pod; leaf T				2	3	
Styphelia Tameiameiae, seed; leaf T					3	
Tephrosia purpurea, seed		3				
Trifolium repens, seed; leaf, blossom T		3	2	1	2	3
Urtica sp., seed			2		3	1
Verbena litoralis, seed			3	3	G	
Vicia sativa, seed			3			
Waltheria americana, seed; flower, seedling T	2	2				
ANIMALS						
Agrotis ypsilon, larva; adult			3	3	2	2
Arachnida (unid.), adult		3				
Blapstinus dilitatus, adult	2	3	3	3	3	
Bruchus sallaei, adult	3					
Camponotus variegatus hawaiiensis, adult	3	3				
Carpophilus humeralis, adult	3					
Cirphis unipuncta, larva					2	
Coleoptera (unid.), adult	3		3	3	3	G
Conoderus exsul, adult; larva T			3			
Curculionidae (unid.), adult					3	
Dermaptera (unid.), adult					3	
Diplazon laetatorius, adult						3
Elateridae (unid.), adult					3	
Hemiptera (unid.), adult; nymph T		3	3		3	
Hymenoptera (unid.), adult						3
Insecta (unid.), adult					3	
Lepidoptera (unid.), larva				2	3	3
Limacidae (unid.), adult					3	
Lumbricus sp., adult					3	
Miridae (unid.), adult					3	
Nesomicromus vagus, adult				3		
Nysius coenosulus, adult			3	3	3	3
Oechalia pacifica, adult				3		
Pantomorus godmani, adult					3	
Sarcophagidae (unid.), adult					3	
Tenebrionidae (unid.), adult						3

[1] T = trace. G = occurrence in gizzard only.

1918; Sumner, 1935; Glading, Biswell, and Smith, 1940). The latter authors found animal food in appreciable proportions only in females that contained developing ova and believed it possibly served a special physiological need. In Hawaii, insects were eaten in approximately equal amounts by both sexes from March through November, which period includes a large portion of the breeding season. The few birds collected during the remaining months were without animal matter in their crops and gizzards, but it is probable that insects are taken

during this period since they are available in most ranges of quail in Hawaii throughout the year.

TABLE 10

FOODS OF CHICKS BY VEGETATION ZONES

Species	*Per cent crop volume* Zone C_2[1]	Zone E_1[2]
PLANTS		
Medicago hispida	40.4	0.6
Hypochaeris radicata	19.2	0
Cirsium vulgare	1.9	54.9
Centaurea melitensis	T	0
Oxalis corniculata	T	0
Setaria geniculata	T	0
Sida rhombifolia	T	0
Sporobolus capensis	T	0
Stellaria media	T	0
Waltheria americana	T	0
Medicago lupulina	G	0
Vicia sativa	0	G
Unidentified plant material	G	T
TOTAL	61.5	55.5
ANIMALS		
Blapstinus dilitatus	28.9	0
Siphanta acuta	9.6	0
Nysius coenosulus	T	10.2
Cirphis unipuncta	0	34.3
TOTAL	38.5	44.5

[1] Total crops, 2
Total gizzards, 2

[2] Total crops, 2
Total gizzards, 2

Seeds and browse constitute the main portion of the diet, as shown in Figure 1, and the relative amount of each, taken in the different vegetation zones, reflects their comparative availability in the range which generally varies but little from month to month. Seeds form a large percentage of the diet only where permanent water is available, as was the case in those portions of zone A where our collections were made. In zones B, C_2, E_1, and E_2, surface water is generally unavailable and browse is substituted according to its abundance. The small amount of seeds eaten in zone D_3 represents an absence of seed-producing plants utilized by quail, due to heavy rainfall, inadequate sunshine, and acid soil.

In California, consumption of seeds and browse is likewise related to availability, although there is a marked change in the diet through the year. Seeds are eaten primarily from April through November while greens comprise the major food during the rest of the year. Birds seem to prefer seeds and will readily take any that are available (Sumner, 1935; Glading, Biswell, and Smith, 1940; Emlen and Glading, 1945).

Foods of chicks.—Only four California Quail chicks, from two to seven weeks of age, were collected. Their foods are given in Table 10. With the exception of two plants, *Centaurea melitensis* and *Setaria geniculata*, and one insect, *Siphanta acuta*, which were eaten only by chicks, the foods were of the same species as those taken by older birds. Insects represent 38.5 per cent of the foods in zone C_2 and 44.5 per cent in E_1. Sumner (1935) reported in California that animal matter constituted 34.5 per cent of the diet of five chicks six to seven days of age.

Grit.—Particles of well-rounded or angular basalt, olivine, quartz, feldspar, and coral were utilized as grit. Individual pieces varied from one-eighth to three millimeters in diameter, with those from one-half to two millimeters being the most common. Grit occurred,

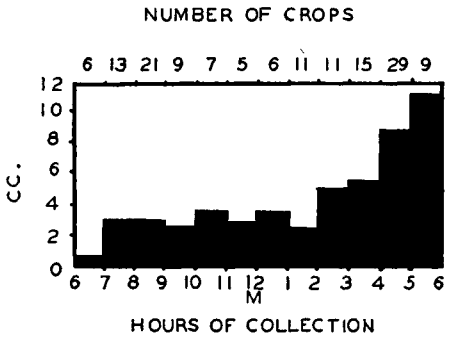

FIGURE 2.—Food volumes in crops of California Quail collected throughout the day.

as a trace, in only one crop but was found in 116 of 132 gizzards examined. Breeding females on the average contained more grit than non-breeding females or than males averaged during March, April, and May.

The percentage of gizzards containing grit varied directly with the amount of browse. In zone D_3 where browse constituted 90 per cent of the food, all gizzards contained grit which averaged 0.54 cubic centimeters in volume. Zone A showed the fewest gizzards with grit and the least amount of browse. In this zone, grit averaged 0.22 cubic centimeters per gizzard. Grit probably functions in the utilization of browse, while seeds tend to grind each other.

Seeds of *Malvastrum coromandelianum* were found more often in gizzards in zone A than in crops; these may represent seeds hard to digest or retained for grinding purposes. All seeds, even very hard-

coated ones like *Sophora chrysophylla*, *Dodonaea viscosa*, and *M. coromandelianum* were found in various stages of digestion in the gizzard. Thus, few if any seeds pass intact through the digestive tract.

Feeding periods.—Figure 2 presents the volumes of food in crops of birds collected at different hours of the day. Field observations on feeding birds agree with these data and indicate causal feeding each day until mid-afternoon when an intensive feeding period begins and continues until dusk. The maximum crop volume was 20.3 cubic centimeters, but the average for full crops taken between 5 and 6 p. m. was 11.2 cubic centimeters. In California, feeding is reported to be less pronounced during midday than during the morning or afternoon (Sumner, 1935; Glading, Biswell, and Smith, 1940).

PARASITES AND PREDATORS

Very few California Quail collected during this study harbored external parasites, and in all cases the infestations were light. When present, mites (*Xoloptes sp.*) were most numerous in the head region. *Mallophaga* were represented by *Goniodes mammilatus* Rudow, *Menopon fulvomaculatum* Denny, *Lagopoecus docophoroides* (Piaget), and *Goniodes sp.* and *Menopon sp.* larvae. Two fleas, possibly *Echidnophaga gallinaceae* (Westwood), the stick-tight flea common to island poultry, were seen on one bird but escaped.

Since many of the internal helminth parasites of gallinaceous birds have insects as their intermediate hosts, the absence of such parasites in California Quail is quite obviously related to the generally low insectivorous diet and to the fact that those insects eaten by quail in Hawaii have not been recorded as intermediate hosts of any internal parasites common to gallinaceous birds. The significance of this relationship is graphically portrayed when foods of the California Quail are compared with foods of the more insectivorous pheasant occupying the same general range. The pheasant is moderately parasitized by helminth forms which utilize as intermediate hosts many insects it eats.

Rats, feral cats and pigs, and mongooses, *Herpestes javanicus auropunctatus* (Hodgson), are the most likely predators upon California Quail because of their general abundance in the range of this bird. Of these, the mongoose is popularly considered a decisive factor adversely influencing quail, but our evidence does not support this opinion. A comparison of populations of the California Quail on islands with the mongoose (Maui, Hawaii, and Molokai) and on islands without the mongoose (Kauai, Lanai, and Niihau) shows only that similar densities occur regardless of the presence or absence of

this predator. Our analysis of 86 mongoose scats, taken mostly from areas occupied by the California Quail, disclosed no remains of this bird. We feel that populations of quail usually reflect the quality and quantity of suitable water, food, and cover as well as climatic conditions rather than the influence of the mongoose or other predators.

BREEDING

Figure 3 presents the distribution and average of testicular volumes in cubic millimeters by month for 66 California Quail, both adults and birds of the year past their post-juvenal molts. There was no correlation between testicular volume by month and the two age classes included in this group; hence, they are considered together. Assuming that spermatogenesis coincides with the rapid increase in testicular weight (which is generally comparable to volume) as occurred in wild pheasants in Montana (Hiatt and Fisher, 1947), the data in this figure indicate that male California Quail are probably capable of breeding in February or March. During March, those males collected with large testes (over 385 cubic millimeters) were found paired with females and in groups of four or eight, while those with smaller testes were in coveys of males and females containing from 12 to 45 birds and exhibiting no pairing. During April and May, males with large testes were only found paired with females, while those with smaller testes were still in coveys composed of 10 to 30 birds, likewise of both sexes. By June, all but one of the birds collected had small testes, probably indicating a regression of spermatogenesis, and were found in coveys of adults only or of adults and their broods, sometimes of varying ages. The one bird with large testes was solitary and actively calling, possibly signifying a continued ability and interest in breeding. The small volumes of testes during the rest of the year presumably represent a cessation of breeding.

The percentage of females breeding (determined by the presence of maturing Graffian follicles) is given by month for 57 specimens. During March, April, and May, all but one female showed Graffian follicles, although the development of the follicles varied with the individual. In some, fully formed eggs were found in oviducts and, in others, enlargement of the oviduct indicated recent laying. After May, no females with developing ova were found.

Newly hatched birds were observed only from May 23 to July 9, except for one brood of seven young approximately two weeks old, seen on March 26, 1946, at 3,250 feet elevation in vegetation zone C_2. From the ages of all broods seen during this study, the main hatching period was computed to extend from the last week of May to the last

week of June. Even in the year around equable climate of most of Hawaii, it is probable that only one brood is produced a year, with late broods representing renesting.

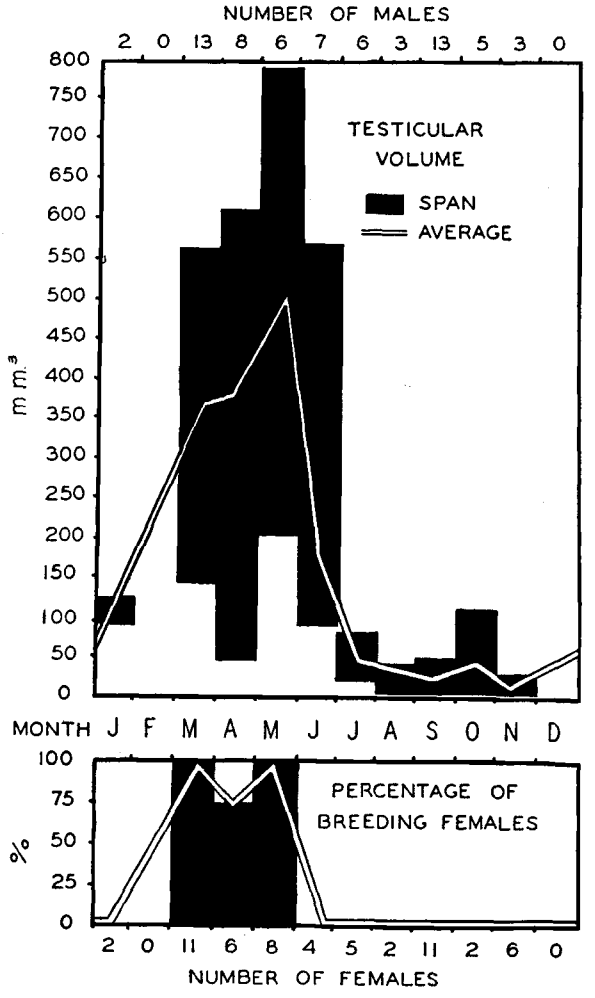

FIGURE 3.—Breeding season of the California Quail as indicated by testicular volume and maturing Graffian follicles.

In January, calling by male birds begins to be common throughout the day. This indication of the approaching breeding season comes about a week earlier at lower elevations; also, breeding activities in Hawaii begin about a month before those in California (Sumner, 1935)

which might be expected because of the differences in latitudes of these respective ranges. Field observations on the breeding behavior of adults and occurrence of chicks, and calculations based upon the gonadal development shown in our limited collections, indicate that, in general, nests are built toward the end of March. Laying occurs in the first three weeks of April and is followed by incubation from the last of April through most of May.

The sex ratio of 145 California Quail collected throughout the year was 77 males to 68 females or, expressed in a standardized manner, 113 males to 100 females. Sex ratios reported in California are identical (Sumner, 1935; Emlen, 1940).

Throughout this study we found low ratios of birds of the year to adults, both in breeding and post-breeding populations. In vegetation zone E_2 in the vicinity of Pohakuloa, Hawaii, the ratio of 22 birds taken during the breeding season of 1946 showed 83 birds of the year to 100 adults. Seventeen birds taken during November, 1946, in this same area showed a ratio of 54 birds of the year to 100 adults. Reliable reports from hunters in other parts of the islands, and our collections from scattered localities at this time, indicated similar low ratios of birds of the year to adults. In California, an average fall population is composed of 165 birds of the year to 100 adults, but variations from 365 to 85 birds of the year to 100 adults have been reported, depending upon the locality and year. By the beginning of the breeding season, the ratio nears equality (Emlen, 1940; Glading, Selleck, and Ross, 1945). In spite of the small samples in Hawaii, it is evident that replacement by young is definitely poor although adult survival seems good.

The amount of rainfall is one of the most important factors influencing reproductive success in Hawaii. It is highly significant that in very dry portions of the range, coveys of 12 to 45 birds occur throughout the breeding season, showing an abnormal condition with respect to pairing and separation of the coveys. A similar phenomenon and failure to breed has been shown in California to result from a shortage of green vegetation, caused by drouth during the pre-breeding season (Sumner, 1935). In Hawaii also, nests located advantageously with respect to succulent vegetation during periods of good growth may have conditions altered by drouth before the brood is produced or raised. However, the chance of inadequate rainfall in two or three successive years in these critical periods is not great, and thus the population is able to maintain itself. Conversely, in higher rainfall areas, the long periods of brooding required in misty weather may prevent adequate foraging by the young, or over-exposure of the

young to mist and rains may cause considerable loss. Because rainfall varies from one zone to another, years of poor reproduction are not simultaneous over the islands as a whole.

As a result of these findings, intensive management for quail, stressing water development, was inaugurated in the Pohakuloa area of Hawaii in 1947 and completed prior to the 1948 breeding season. In 1948, hunting reports here (Smith, MS, 1948) showed a ratio of 254 birds of the year to 100 adults in a take of 239 quail, probably indicative of a good breeding season and doubtless influenced by this water development.

RANGE EVALUATION

Zone A.—Zone A occupies the coastal flats and adjacent sloping lands from sea level to elevations generally less than 1,000 feet on lee sides or low windward lands. The mean annual temperature at sea level is 75° F. with the maximum often more than 90° F. Rainfall is less than 20 inches annually. The major uses of the land are for irrigated sugar cane and grazing, but considerable waste areas occur.

California Quail range in this zone is restricted to pasture or waste portions. Unoccupied parts generally include wind-blown, sand-dune country on Molokai, undecomposed lava on Hawaii which is often devoid of vegetation, and land in sugar cane on Maui and Kauai.

The aridity of this zone is the greatest factor limiting quail. Although infrequent, the rainfall is usually violent, and on rare occasions more than the average annual precipitation may occur within a period of a few days. Both evaporation and run-off are high, and long periods of drouth result. Because rainfall fluctuates widely from month to month and year to year, the measure of productivity of this zone varies greatly. Quail respond to this environment in a pulsating fashion. They expand to areas made inhabitable by abundant verdant growth which so characteristically follows rains; when drouth sets in again, they retire to the vicinity of water holes or pockets of better growth. Where succulent vegetation is limited or available water absent, adult birds lack moisture during the pre-breeding season and probably fail to breed. Broods hatched in areas where drouth has reduced the succulent vegetation subsequent to the beginning of nesting also suffer. However, where water provided for cattle is constantly available to quail through seepage or overflow, permanent populations of high densities usually occur.

Foods eaten by quail in zone A show 96 per cent seeds, two per cent browse, and two per cent animal matter. Our collections in this zone were made in areas where water was available through springs or

seepage from stock-watering troughs and where quail utilized the seeds which predominated in the vegetative cover. The two class 1 foods, *Prosopis chilensis* and *Leucaena glauca*, are plentiful throughout the range of quail in this zone and form a staple food supply. Where cattle forage on the bean crop of *P. chilensis*, many of these seeds are present in their droppings and quail take seeds from this source. *Portulaca oleracea* and *Waltheria americana*, class 2 foods, are less common in the range than the species in class 1, but they form a substantial food supply for quail.

Domestic livestock and feral goats and pigs compete with quail by foraging on green plants and produce their most inhibiting effect during dry periods when growth is at a minimum. Because the general forage value of plants in zone A is low, even limited grazing exerts considerable influence on food as well as on desirable cover.

On the coastal flats, quail resort to the upper story of dense *P. chilensis* for escape and roosting. Excellent idling cover is also provided in the heavy shade of these trees. In the draws which sustain better green growth than the surrounding land because of moisture accumulation, good protective, roosting, and idling cover occurs where *P. chilensis*, *L. glauca*, and *Acacia farnesiana* grow abundantly. On the slopes, *P. chilensis* is less vigorous but still provides good cover. The major nesting areas probably are on the slopes in the interspersion of the shrubs, *Sida sp.* and *W. americana*, and annual grasses. Although not universal in this zone, *Lantana Camara* offers good protection where it grows.

In the occupied 32 per cent of zone A, amounting to 171 square miles, a population of 11,170 California Quail exist. Densities range from less than 15 to 600 birds per square mile.

Highest densities (from 151 to 600 birds per square mile) occur in the dense *P. chilensis* on the coast of Molokai where the most favorable factor is the frequency with which water holes, natural springs, and windmill-powered wells occur (Plate 1). Although grazing is heavy, a slightly higher rainfall here supports some green growth which furnishes supplementary moisture, and the adjacent slopes provide abundant food. It is further significant that these excellent populations occur away from human habitation.

Where lower densities occur in this zone, water is available only occasionally and rainfall is somewhat lower, resulting in inferior plant growth. Concentrations of birds are found in the immediate vicinity of water holes, but large populations are not produced because of the small area served by each source.

In parts of zone A, predation by mongooses may be an important

factor influencing populations of quail. Rats are numerous where they can feed on seeds of *P. chilensis* and find good nest sites in the branches of these trees or in near-by rocky outcrops. Illegal shooting adversely affects quail along main roads.

Zone B.—Zone B lies above zone A where it is present and reaches approximately 2,000 feet elevation; on low windward lands it may occur at sea level. Approximately 70° F. is the mean annual temperature for this zone. Rainfall varies between 20 and 40 inches annually. Cultivation of irrigated sugar cane occurs below 1,200 feet elevation, while pineapples are raised above this contour. Grazing lands (Plate 1) and waste areas constitute the remaining uses of this zone.

Like zone A, aridity is believed the major factor limiting quail. However, a slightly increased rainfall in this zone provides a more varied and vigorous plant coverage. This number of plants is reflected in the diet of quail, of which seeds compose 85 per cent, browse 15 per cent, and animal matter only a trace. *Cassia Leschenaultiana*, the only class 1 food in the range, is common and provides a staple source of food. Eleven species are considered as class 2 foods indicating the variety of plants available, as well as utilized, for food. *Lantana Camara* and *Opuntia megacantha* often occur in dense stands and limit occupation by quail, but where they are part of a desirable interspersion these species provide valuable cover.

Thirty-four per cent or 267 square miles of zone B is occupied by an estimated population of 12,280 California Quail. Densities from the lowest to highest class occur.

Highest populations (301 to 600 birds per square mile) occur on Molokai and are continuous with an equal density in zone A. Lower densities are found under two types of conditions, primarily on Hawaii: (1) Where pasture grasses and herbaceous forage plants are plentiful because of somewhat increased rainfall, but suitable cover is limited; and (2) where *Metrosideros collina* var. *polymorpha* and other native trees are abundant on lava flows and in conjunction with the irregular lava furnish excellent cover, but desirable food is lacking.

In all ranges of this zone, heavy grazing by cattle and feral goats reduces desirable forage and cover plants. Predatory species are the same as in zone A.

Unoccupied portions consist of pineapple or sugar cane land, barren lava flows, homestead or urban areas, extensive stands of *L. Camara*, or very open pasture land.

Zone C_2.—This zone includes the steeper mountain gradients and high plateaus between 2,500 and 4,000 feet elevations. The mean annual temperature of approximately 60° F. is too cool for sugar cane

or pineapple culture so grazing is the major land use. Rainfall limits lie between 40 and 60 inches annually, and this precipitation is fairly uniformly distributed throughout the year, providing adequate moisture for good plant growth.

A population of 10,590 quail occurs in 294 square miles, representing 76 per cent of the zone. Densities vary from less than 15 to 300 birds per square mile.

The factor limiting the populations of quail is undoubtedly lack of suitable shrubs and trees necessary for roosting and, to a lesser extent, for escape and idling since much of this zone consists of open grassland. Heavy grazing further reduces what cover could be supplied by this grassland.

Food studies show the diet consists of 36 per cent seeds, 63 per cent browse, and one per cent animal matter. *Hypochaeris radicata* and *Medicago lupulina* of class 1, and *Cirsium vulgare* and *Bromus catharticus* of class 2 are common plants in this zone; combined, they form a staple supply of food because they furnish both seeds and browse.

Highest populations are found in those portions with suitable cover provided by *Metrosideros collina* var. *polymorpha* and other native trees on "*aa*" lava flows or by an interspersion of the shrubs, *Dodonaea viscosa* and *Styphelia Tameiameiae*, grasses, legumes, and other herbaceous forms with occasional windbreak plantations of *Eucalyptus sp.* and *Cryptomeria sp.* An absence of suitable cover results in low densities although food and available moisture seem adequate. Predation appears unimportant in the zone as a whole.

Unoccupied portions consist of badly eroded slopes traversed by numerous lava flows and heavily grazed by feral goats, extremely open grassland, or barren lava.

Zone D_3.—This zone lies between 4,000 and 7,000 feet on windward sides and has a mean annual temperature of about 50° F. Grazing is the major agricultural use. Rainfall varies from about 100 inches at lower elevations to 50 at higher limits.

Seventy-eight per cent of this zone, some 302 square miles, is occupied on Maui and Hawaii and has a combined population of 5,880 birds. Densities vary from 75 to less than 15 birds per square mile.

California Quail live in the open *Acacia Koa* forests but not in barren lava, extremely open grassland, or densely-forested sections. Since a large part of the precipitation occurs as mist during both day and night, the general climate is damp and cool. This seriously affects young quail by preventing them from foraging, because during periods of mist they are brooded by the hen. In parts of California, fog occurs practically every summer night from about 6 p. m. until 9 a. m. the

following day, but these conditions produce no visible ill effect upon quail (Sumner, 1935). However, it is believed by Sumner that it would be impossible for quail to breed successfully in a region where fog does not disappear long enough each day to allow adequate foraging by the young.

Highest populations occur where the cover is primarily of *Acacia Koa* trees with an undergrowth of ungrazed or moderately grazed native shrubs, grasses, herbs, and ferns. Under extensive grazing by domestic stock and feral pigs and goats, only remnant stands of trees and sparse undergrowth result. California Quail are limited in number in these heavily-grazed areas (Plate 1) and in densely-forested sections.

Foods in zone D_3 show 90 per cent browse, nine per cent seeds, and one per cent animal matter. *Hypochaeris radicata* and *Trifolium repens* furnish most of the browse. The lack of sunshine and a dry season, coupled with other unfavorable factors such as acid soils and extensive grazing, result in an absence of seed-producing plants desired by quail. This shortage of suitable protein may affect fertility of adult birds and, together with the heavy precipitation, may inhibit reproduction by California Quail in this zone.

Zone E_1.—Zone E_1 occupies high plateaus and gentle mountain slopes between 4,000 and 7,000 feet elevation. The mean annual temperature is about 50° F., and rainfall is approximately 40 inches annually. Frost occurs occasionally at lower elevations and ice forms in upper areas. Grazing is the only economic use of the land.

This vegetation zone has the most extensive area occupied by quail (585 square miles), the highest percentage of any zone occupied (85 per cent), the highest population (25,530), and densities ranging up to the highest (600 birds per square mile). Diversified food and cover conditions, accompanied by adequate moisture in the form of browse, combine to give this zone great potentialities for California Quail.

Food studies show the diet consists of 57 per cent browse, 33 per cent seeds, and 10 per cent animal matter. Class 1 and 2 foods are generally plentiful in the range and provide a satisfactory source of both browse and seeds.

Heavy grazing by controlled livestock and feral sheep and goats is the factor limiting food and cover for quail in this zone.

Highest densities (from 151 to 600 birds per square mile) occur in the plateau between Mauna Kea and Mt. Hualalai on Hawaii (Plate 1). Scrubby *Sophora chrysophylla* and *Myoporum sandwicense* provide an ideal interspersion and, coupled with a variety of low shrubs, grasses, and herbs, create a maximum edge. *Dodonaea viscosa* and *Styphelia Tameiameiae* are the predominant shrubs and the native

bunch grasses, *Eragrostis grandis* and *Panicum tenuifolium*, are especially common. Mongooses and rats probably exert little influence, although feral cats originating from the near-by Waikii settlement are comparatively numerous.

Lower densities occur elsewhere for various reasons: (1) The range is principally of open grassland, a result of overgrazing, and lacks proper diversification and quality of food and cover necessary to sustain high populations; (2) Heavy brush and forests on poorer soils provide undesirable cover and limited food; (3) Numerous barren lava flows interspersed with "*kipukas*" (areas by-passed by lava) provide good but limited habitat; (4) Rats, feral pigs and goats, and especially mongooses, are abundant in certain regions.

Zone E_2.—This zone occurs above zone E_1 between 7,000 and 10,000 feet elevation and exhibits a steep topography. The mean annual temperature is about 40° F. and summers are too cool to permit good plant growth. National Park and Forest Reserve are the important land uses, but heavy grazing by feral sheep and goats also occurs.

In 136 square miles, 10,970 California Quail occur with densities ranging up to 300 birds per square mile. However, only 25 per cent of this zone is suitable for occupancy by quail because the little-weathered soil makes a poor substratum for vegetation. Rainfall is less than 40 inches annually and almost all moisture must be obtained from browse. Unoccupied portions of this zone consist of volcanic wastes.

Our food studies show that browse comprises 32 per cent of the dietary, seeds 61 per cent, and animal matter seven per cent. All class 1 and 2 foods are rare in the range with the exception of *Sophora chrysophylla* which forms a staple source. Because of the sparcity of foods for quail, populations are correspondingly limited in distribution.

S. chrysophylla and *Myoporum sandwicense* are the common trees but, although vigorous, are stunted. *Styphelia Tameiameiae*, found associated with these trees, is the predominant plant in areas where the trees have been eliminated by continuous heavy grazing. While creating a certain amount of interspersion, *S. Tameiameiae* tends to become dense in certain areas limiting small herbs and other desirable foliage.

In addition to the restricted grazing by domestic stock, feral sheep and goats exert extreme grazing pressure over most of the range. Aridity and overgrazing are the main factors adversely affecting quail.

The highest densities (151 to 300 birds per square mile) occur in the vicinity of Pohakuloa, Hawaii. Although formerly heavily grazed by feral stock and supporting a low population of quail, protection from

grazing in recent years has resulted in improved food and cover as well as increased populations of quail. Few plants grow in this dry area except beneath *S. chrysophylla* and *M. sandwicense* where moisture is provided by drip from the condensation of infrequent mists and light rains on the leaves. The rate of evaporation is also reduced by the shade from these trees.

Lower densities occur where the same cover species are found, but the range is subjected to the devastating impact of huge numbers of feral sheep. Feral dogs, a minor threat to nesting quail, inadvertently aid the quail by preying upon sheep in this area. Cover and particularly food species do poorly here.

Zones C_1, D_2, and E_3.—Only small areas of these zones adjacent to other occupied regions have California Quail.

Zone C_1 occurs between sea level and 2,500 feet on gentle and steep slopes dissected by deep gullies and on high plateaus. The mean annual temperature is 70° F. Rainfall is between 40 and 60 inches annually. This zone contains the largest proportion of arable land with good quality soil, and good yields of sugar cane and pineapple result. Grazing is restricted to gullies and poorer soils, and little range is available for quail.

Zone D_2 has variable limits of elevation but generally lies between 1,500 and 4,000 feet on windward sides. The mean annual temperature is approximately 60° F., and rainfall is from about 60 to 450 inches and more annually. Forest Reserve, providing the main source of water for the islands, is the major use of this zone although grazing occurs in some cleared portions. The heavy rainfall and associated dense vegetation restrict use of this zone by quail.

Zone E_3 occurs only on Hawaii between 10,000 and 13,784 feet. Temperatures are near freezing and snow is frequent, remaining in sheltered places all year. The precipitation is probably less than 20 inches annually. The main use of this land is for National Park and Forest Reserve. Quail exist only along the fringe of zone E_2 where suitable food and cover species occur and, during winter, descend to about the 10,000 foot level.

Zone D_1.—This zone is unoccupied by quail at present, but some populations occurred on Hawaii and Kauai prior to intensive use of this zone for non-irrigated sugar cane, pineapples, and grazing. Zone D_1 lies between sea level and 1,500 feet elevation on windward sides and has a rugged topography. Temperatures are about 2 to 3° lower than on lee sides at the same elevations and the mean annual temperature is about 73° F. The annual minimum precipitation is 60 inches. The soils are leached, acid, and poorly aerated.

SUMMARY

1. The California Quail was introduced to the Hawaiian Islands from California prior to 1855. Some of these original plantings became established, but sporadic importations continued until 1940.

2. In 1946 and 1947, 1,800 square miles were occupied by California Quail on all of the major islands except Oahu where their occurrence was very rare. Quail also occurred on the privately-owned island of Niihau but no estimate of the total population was available for this island.

3. On Hawaii, only the valley form of the California Quail was found. The coastal form of the California Quail was the sole race collected on Molokai, but birds resembling both races and their intergrades were found in the same coveys on Maui, Kauai, and reported on Niihau. The race on Lanai and Oahu is unknown.

4. The range of the California Quail in Hawaii includes elevations from sea level to 11,000 feet, temperatures ranging from an annual mean of about 75° F. to an annual mean of about 40° F., and variations in rainfall from less than 20 to 60 inches annually; in a few places, rainfall may be 100 inches annually. The habitat of quail occurs on portions of soils used for grazing or without present economic use. The extensiveness and intensiveness of grazing and amount of water available in any form directly influence the presence and density of populations of California Quail. Populations are highest on the most fertile soils within the range.

5. A total population of 78,000 California Quail was estimated for the major Hawaiian Islands, with densities varying from less than 15 birds to 600 birds per square mile. The best ranges occur in vegetation zones A, B, C_2, E_1, and E_2. Vegetation zone D_3 has range of intermediate quality, while poor range occurs in vegetation zones C_1, D_2, and E_3. No quail are found in vegetation zone D_1 although some were present until about 1928.

6. An analysis of 145 crops showed 67 species of plants and 26 animal items utilized as food. Seeds and browse comprised the major food types and varied by vegetation zone in accordance with their availability and that of water. Animal matter occurred in relatively small amounts in the dietary. Foods of chicks and grown birds were generally the same species. Grit occurred only in gizzards, and the amount of grit varied directly with the amount of browse. Feeding is casual throughout the day until mid-afternoon when an intensive feeding period takes place until dusk.

7. Parasitism by external forms was light, and no internal helminth

parasites were found. Predation is not a decisive factor influencing populations of the California Quail.

8. The breeding season begins in January. Nests are built toward the end of March, with laying taking place during the first three weeks of April. Incubation occurs from the last of April throughout most of May, and the main hatching period extends from the last week of May to the last week of June. Low ratios of birds of the year to adults were found in breeding and post-breeding populations, indicating that replacement by young is definitely poor, although adult survival seems good. It is believed that the amount of rainfall is one of the most important factors influencing reproductive success of the California Quail in Hawaii.

9. The range in each vegetation zone is evaluated with respect to productivity of California Quail.

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Conservation Commission, Jefferson City, Missouri, April 5, 1949.

THE SANDHILL CRANE IN THE BERNARD W. BAKER SANCTUARY, MICHIGAN

BY LAWRENCE H. WALKINSHAW

INTRODUCTION

IN September, 1921, I made my first visit to the area now constituting the Bernard W. Baker Sanctuary. Several visits were made to the area during August, 1930, and several during May, 1931. Thereafter, I have visited it nearly every month, often many times during some months. Some of these observations have been published by the author (1933, 1941, 1944, 1945, 1946, 1948). A great deal of information on the Greater Sandhill Crane, *Grus canadensis tabida* (Peters), has been secured on the area. Some of this material has been incorporated in my manuscript on the Sandhill Crane, but a great deal of it could not be used. I am assembling that data in this article.

THE AREA

The marsh in which the Bernard W. Baker Sanctuary area is located consists of approximately 1000 acres. The Sanctuary, purchased during 1941 by Bernard W. Baker of Marne, Michigan, and presented to the Michigan Audubon Society, consists of 571 acres. About 71 acres are on high land and land connecting the area to highways. The marsh lies in sections 10, 11, 14 and 15 in Convis Township, Calhoun County, Michigan.

The marsh consists of many irregular sedge and grass-grown "arms" reaching through forests of: tamarack, *Larix laricina;* maple, *Acer;* birch, *Betula;* ash, *Fraxinus;* basswood, *Tilia americana.* Some elm, *Ulmus*, and hickory, *Carya*, are found on the ridges or in swampland woods. One ridge of dry land is covered with second growth oak, mostly white oak, *Quercus alba*, with some black oak, *Quercus velutina* and red oak, *Quercus borealis maxima.* This ridge extends from the northeastern corner of the marsh over one-half mile toward the center. Another island occurs in the northwest corner and a third near the